The American Midland Naturalist

Devoted to Natural History,

Primarily that of the Prairie States

Founded by J. A. Nieuwland, C. S. C.

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The American Midland Naturalist

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THE PLANT ASSOCIATIONS OF CENTRAL LONG ISLAND

A STUDY IN DESCRIPTIVE PLANT SOCIOLOGY

HENRY S. CONARD

FOREWORD

This study is an attempt to apply some of the recent methods of Plant Sociology to the description of the vegetation of a circumscribed area. The works of both American and European ecologists have been quoted and compared. Previous studies in this area have been cited and summarized. It is intended to place in the hands of workers at the Long Island Biological Laboratory a record of the present state of our knowledge of the region from the sociological viewpoint. In spite of its manifest incompleteness, it is hoped that this report may serve a purpose.

The lists, tables, and charts are the work of students at the Biological Laboratory from 1927 to 1934 inclusive, supervised and critically checked by the senior author. Naturally the experience and observations of the same author in six weeks work in each of the summers of 1909, 1910, 1911, and 1922 have been drawn upon.

Names of plants follow Gray's Manual so far as given therein. Moss names are taken from Grout, and algae from Hylander's Algae of Connecticut.

Appreciation for facilities afforded, and for aid rendered, is especially due to the Executive Committee and the Director of the Long Island Biological Laboratory, and to my colleagues in the summer school, Dr. F. K. Sparrow, Dr. A. W. Blizzard, Miss Louisa Sargent, Dr. Stanley A. Cain, and Dr. A. J. Grout. Other personal acknowledgments appear in the text.

Part I.—Introduction

1.—LOCATION OF THE AREA

Geographic.—The Jones Laboratory of the Long Island Biological Association is located at approximately 40° 51′ 36″ N. and 73° 28′ 51″ W. (see map Fig. 1). The laboratory property lies on the west side of the inner (southern) end of Cold Spring Harbor, on the north shore of Long Island, about 30 miles from New York City. The points studied in detail for this paper fall within an area bounded on the west by a line from Hempstead Harbor to Long Beach, and on the east by a line from St. James to Lake Ronkonkoma and Great River. The "towns" (townships) of Oyster Bay and Huntington have furnished most of our material.

Floristic and Sociologic.—The Biological Laboratory is situated about midway of the eastern border of the floristic area covered by Gray's "Manual of the Botany of the Northeastern United States and Canada." The flora of the area is therefore well supplied with both northern and southern species. The

richness of the flora is enhanced by a variety of edaphic and microclimatic conditions, giving place to a multitude of different plant associations.

From the standpoint of sociological plant geography, our area is in the Long Island subdistrict of the North Atlantic District of the Coastal Sector of the Western Atlantic Province of the Euro-sibiric-North American Vegetational Region.

This subdistrict includes representative stands of a number of plant associations, alliances, and orders. The Littoral communities of Schimper are

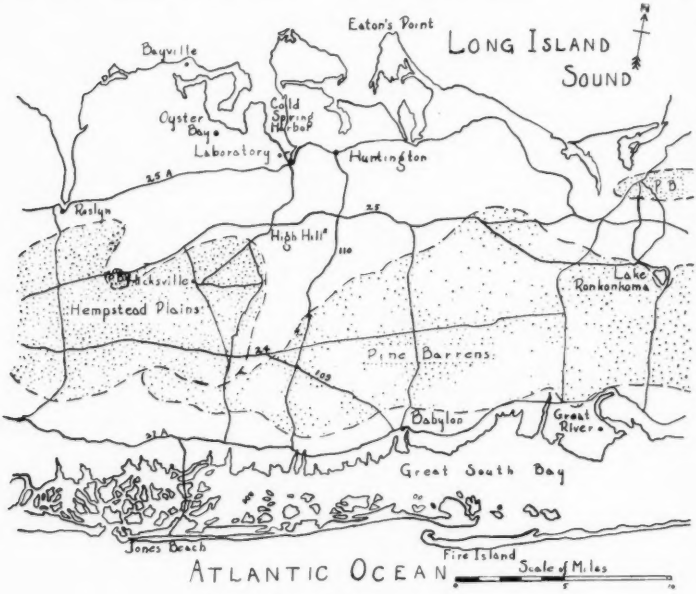

Fig. 1. Map of Central Long Island.

admirably displayed both on the shores of Long Island Sound and on the ocean front. The Oak-Chestnut (now mixed oak) forest of Shantz and Zon (1924) is well developed on the north shore hills. The Oak-Pine forest is characteristically shown in the middle of Long Island, in the so-called Pine Barrens. Pond, stream, and swamp associations of the two forest "formations" are shown. Cool north slopes of the north shore hills harbor fragmentary associations of the Beech-Maple forest. A remarkable area of natural grassland, the Hempstead Plains, occupies the western center of our area. This prairie has long been a curiosity to ecologists, and a reservoir of "rare" plants for systematic botanists. Thus, a study of our area brings into review all of the characteristic vegetational "formations" of the northeastern United States.

The most serious studies of the plants of this region are "The Relation of Plants to Tide Levels" by D. S. Johnson and H. L. York, and the "List of plants growing without cultivation in the vicinity of Cold Spring Harbor" by N. M. Grier. Johnson and York have presented in great detail the vegetation of the "inner harbor" below the level of the flood tides. They have shown a clear relation of the plants to the tide levels, and interpreted their findings as due to the daily period of exposure of the plants to sea water or to air.

Grier's list, followed by a list of the cultivated plants, is an extensive and useful compilation, even though there are several misprints and mis-arrangements, and some of the plants claimed are certainly not here in a wild state. Other papers are cited in appropriate places, or included in the bibliography.

2.—History

Geologic.—The hills about Cold Spring Harbor are composed of loose gravel and sand, the so-called Harbor-Hill Moraine, of Wisconsin age. Directly south of the Laboratory about two miles, the "Ronkonkoma Moraine" branches off from the Harbor-Hill Moraine and runs out toward Montauk Point. High Hill (420 ft.) is in the Ronkonkoma Moraine, and is also composed of gravel. Numerous sinks and ponds, presumably caused by the melting of buried masses of ice, dot the surface of both moraines. The largest of these kettles is Lake Ronkonkoma, 20 miles east of the Laboratory. South of the moraines, and sometimes cutting through the southern (and doubtless older) one, there are great flat outwash plains, made up of fine sand or gravel, and sloping imperceptibly to tide level at the south. A narrow barrier-beach, cut by inlets at intervals of from 5 to 15 miles, lines the south side of the island, blocking the waves and winds of the Atlantic. Between this and the mainland, an area 1 to 5 miles wide is occupied by countless level islands of saltmarsh grasses, and a great shallow brackish inland sea, with many square miles of *Zostera marina*.[1]

Underlying the glacial gravels and interbedded with them at various depths are masses, perhaps continuous beds, of sticky cretaceous clays, such as crop out at Gay Head on Martha's Vineyard.—"they markedly influence the circulation of underground water." "Aside from their effects on the circulation of underground water they do not influence the agriculture of the country." (Bonsteel, 1904, p. 10).

The so-called moraines are more properly deformed cretaceous gravels and clays, oozed up by the weight of the ice, rather than dumped by the glacier. This is clearly seen in brick yards all along the north short from Flushing to Port Jefferson, and at some inland places. The only unmistakable till is a rather thin sheet (3-10 ft.) overlying these beds.

The north shore in our area consists of a row of gravel headlands, portions

1 *Zostera* was totally absent in the summer of 1932, as elsewhere along the Atlantic. It has not returned (1934). This has wholly changed the biotic relations of these waters with serious effects uopn the oyster industry. Cf. Association 7, following.

of the dissected moraine. Many of these were at one time islands, but are now joined to the land by narrow bars of sand. This gives the system of deep and branching bays and harbors of the north shore. At many points the headlands are now suffering active erosion by the waters of Long Island Sound. At such points, lines of huge boulders, residue of glacial drifts, run far out into the water. Between these points, long stretches of sandy beach occur. The beach may lie at the foot of a bluff, or may merge into a sandy plain, or may be cut by channels leading into saltmarsh areas.

The exact age of the outwash plain south of the moraines is uncertain, nor are geologists agreed about changes of level of land and sea. Ward (1920) states that the land about New Haven, Conn., stood some 200 ft. higher above sea-level during the last glaciation than at present. If that be true, Long Island must also have been at a relatively higher level, and the land area would have extended much farther to seaward—perhaps 50 to 70 miles —than at present. This is a very important matter for the botanist, since such a land area would support an extensive flora. And the present vegetation of the Island must have a very definite genetic relation to that flora. Unfortunately no fossil evidences are known on Long Island. The only knowledge that we have of a vegetation preceding our own is the finding of a pine cone *(P. strobus)* and a hemlock cone *(Tsuga canadensis)* three feet below the surface of Woodbury Bog, by Mr. Henry Hicks. This would be of relatively recent age—perhaps only a thousand years.

Secular.—The shores of Cold Spring Harbor were first settled in 1705 by a group of Englishmen from the neighboring settlement of Hempstead Harbor. While the country around was gradually cleared in part and cultivated, much remained in timber. Wood was cut for local purposes, and much was sent to New York for fuel. Later, the Harbor became a ship-building center. Here Paul Jones fitted out the first American Navy. In Revolutionary days the drumhead factory, still operating east of Cold Spring Harbor depot, was a flourishing industry. Whaling ships made their headquarters in the harbor. The settlement was the market for whalers' supplies, as for their products. A grist mill served both Long Island and the states across the Sound. The mill was run by water power; hence the three fresh water ponds (dams) up the valley. These ponds are so old as to present essentially natural vegetation around their margins, especially at their inlets. A cotton mill operated at one time, driven by this same water power. About 1859[2] a railroad was projected to run to the harbor. After the cuts and the fills were about completed, the project was given up. Thus a mile or so of denuded morainal gravel was left to be reclothed by natural processes. With all of these activities, there are no introduced plants which are peculiar, or attributable to industrial wastes. The Locust *(Robinia pseudo-acacia)*, which is very abundant everywhere, was purposely introduced for shipbuilding purposes about 1705 at Sands Point, L.I. It is said to have been purposely carried to Cold Spring Harbor. This is the tall, straight-trunked, seedless "yellow"

2 Cf. John H. Jones: History of the Jones Family of Long Island.

locust, with the most durable wood. *Ailanthus glandulosa,* introduced soon after its advent to America, has become abundantly naturalized. The ordinary introduced plants of the northeastern United States are here in the usual proportions, and many less usual species have escaped in the last thirty years from gardens round about. But the remarkable feature of the region is the very large amount of essentially or wholly natural vegetation. The extensive forested areas have long been held in large estates, with a very little selection cutting. The Pine Barrens, Hempstead Plains, and Littoral regions have been mostly untouched because of infertility. But the suburban home, the outing place, and improved methods of farming are rapidly encroaching upon even the most inaccessible and sterile places.

3.—Climate

Long Island lies near the southeastern corner of the BC'r Climatic Province and of the c sub-province of Thornthwaite (1931), that is, it is humid and microthermal, with precipitation adequate for plant life at all seasons, and with somewhat over 50% summer concentration of thermal efficiency. The details of the climate of the Island have been treated in a 20 page brochure by Norman Toylar (1927). Rainfall over a period of eleven years is discussed by Conard (1924b) in relation to the vegetation of the saltmarsh. From Taylor's paper the following data for Roslyn are taken, this being the nearest to Cold Spring Harbor of the stations he cites.

Temperature.—Mean annual	Mean maximum	Mean minimum
At Roslyn 51.0°F.	60.6°	41.6°

Yearly effective temperature[3] 4274°.

Effective temp. before May 1 649°.

Frostless period Av. 187 days; shortest 158; longest 217.

Flowering of lilac 1926 (Garden City) May 20th.

Effective temperature at Roslyn by months: April 162°; May 487°; June 717°; July 924°; August 894; September 663°; October 406°; November 21°.

Direct summation of normal daily mean temperatures for period of average frostless season (New Haven, Conn.):

Above 0°F. 11,560; above 32°F. 5,800; above 39°F. 4,540; above 50°F. 2,740.

Last killing frost in the spring (Roslyn) Av. Apr. 23. Latest known date May 11. First killing frost in the autumn (Roslyn) Av. Oct. 27. Earliest known date September 29. Lowest known temperature:—14°F., Feb. 9, 1934.

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3 "Computed by multiplying the number of days with a mean temperature above 42°, by the number of degrees of temperature in excess of that figure." Taylor, p. 7.

Maximum Long Island Temperatures

1919	July	3- 6	4 days average max. 98.5°
1923	June	20-21	2 days average max. 99.5°
1926	June	4- 6	3 days average max. 95.5°

Precipitation.—

Av. annual (Roslyn) 45.72 in.

Jan. 4.01 in.; Feb. 3.58; Mar. 4.08; *Apr. 3.75; May 3.81; June 3.51; July 3.93; Aug. 4.85; Sept. 3.59; Oct. 3.17; Nov. 3.00;* Dec. 4.44

Precipitation during the period of effective temperatures (Roslyn) underscored; total 29.61 in.

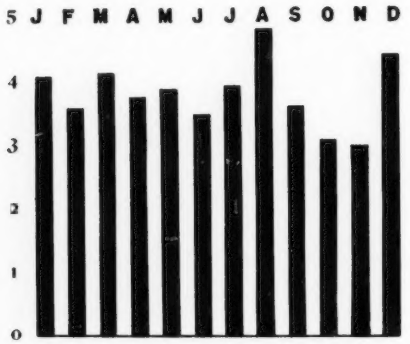

Fig. 2. Average precipitation in inches for each month. Roslyn.

Minimum summer rainfall

1910	July	0.23 in.	1914	Sept.	0.20 in.
	Sept.	1.43	1916	Aug.	0.59
1912	June	1.17	1923	Aug.	1.12
1913	June	1.43	1924	July	1.30

These figures give an idea of the irregularity hidden under "mean" or "average" precipitation.

The average annual precipitation is remarkably evenly distributed throughout the year (Fig. 2). This makes the stress even more severe in the occasional periods of extreme drought and heat (26 times from 1873 to 1925). Such a period fell in June and July 1929, and again in 1934.

Evaporation.—In 1906-07 Transeau (1908) measured evaporation by means of Livingston atmometers at thirteen stations in the vicinity of the Biological Laboratory. The numbers in the table given below are copied from Transeau's paper. An instrument in a low-lying cultivated garden (station 1) was arbitrarily chosen as the standard, with which all others were compared.

At each station from 1 to 4 readings were made, covering periods from 8 to 27 days (84 days at station 1). The readings do not always cover continuous periods. For example station 6 was studied from June 5 to July 2 consecutively; but station 11 was studied from June 14-23 and August 5-12, a total of 14 days.

TABLE 1

Relative Evaporation in different Habitats.
Adapted from Transeau (1908)

Station	Total Evap.	No. of days	Percent	
1.	1657	84	100	Cultivated garden 3 m. above sea level.
2.	336	19	79.6	Cultivated garden 40 m. above sea level on hills.
3.	319.9	16	100.8	Mobilideserta: Gravel slide 25 m.
4.	190.0	16	59.5	Mobilideserta: Gravel slide 25 m.
5.	71.6	8	52.2	Quercetum prini.
6.	229.0	27	40.1	Quercetum Kalmietosum.
7.	18.5	9	13.0	Quercetum moist.
8.	41.0	18	9.9	Liriodendretum, wet.
9.	332.1	22	78.2	Ammophiletum or Hudsonietum.
10.	251.1	13	88.6	Ammophiletum or Hudsonietum.
11.	346.4	14	127.5	Spartinetum ecotone.
12.	112.8	8	86.9	Spartina patens-Scirpus americanus ecotone.
13.	57.0	8	43.9	Aspidietum Thelypteris.

The habitat factors for the associations of the "Inner Harbor" are given in minute detail by Johnson and York (1915).

Wind.—The total wind movement is slightly over 80,000 miles. "—Evaporating power of the air is without regional significance on Long Island" generally (Taylor, 1927, p. 18-19).

Approach of spring and descent of winter.—Long Isalnd has a distinctly insular climate. The yearly range of temperature from lowest to highest is relatively small. Still more is this true of monthly and daily ranges. The autumn days grow gradually cooler until the frost strikes, thus inducing timely ripening of both deciduous and perennating organs of plants. The range between maximum and minimum temperatures is greatest in October, being 20 degrees. Similarly the spring warms up gradually. The monthly mean temperatures are: Feb. 28.8°; March 38.1°; April 48.4°; May 58.7°; June 66.9°. The range between mean maximum and mean minimum temperatures in May, June and July is about 22°; in March 19°; in April 20° (Roslyn). The lowest known temperatures (–14°F.) find vegetation fully at rest.

A snow blanket, fogs, and the proximity of the sea, all tend to soften the effects of below-zero temperatures, which the records show in any case to be of brief duration and rather rare occurrence (Taylor 1927, p. 10).

4.—Soils

A recent survey of Long Island by Clarence Lounsbury et al. was published in the report of the field observations of the Bureau of Soils, United States Department of Agriculture, for 1928. According to this report, our area has representatives of 26 types of soil:

Beach sand
Dune sand
Peat
Dukes loamy sand
Dark colored phase of Dukes loamy sand
Bridgehampton loam
Bridgehampton loamy sand
Plymouth sandy loam
Plymouth fine sandy loam
Steep phase of Plymouth sandy loam
Sassafras loam
Made land
Tidal marsh
Meadow
Babylon sand
Dukes sand
Haven loam
Northport loam
Bridghampton silt loam
Mineola gravelly sandy loam
Plymouth loamy sand
Plymouth sand
Plymouth gravelly sandy loam
Sassafras fine sandy loam
Hempstead loam

Most of these soil types are not precisely correlated with the vegetation types. The Beach-Dune communities occupy the Beach sand and the Dune sand. The Tide marsh land is covered by saltmarsh. The Oak-Pine communities (Pine Barrens) occupy the Sassafras sandy loam, the Sassafras loam, Dukes loamy sand, and Babylon sand, but the boundaries of the soil types and the Oak-Pine associations are not coincident. Hempstead loam, Haven loam, and Sassafras loam in their vicinity are covered by the tall grass prairie of the Hempstead Plains *(Andropogonetum Hempsteadi)*, but again the boundaries are not coincident, as they are reported by the soil survey on the one hand and plant ecologists on the other. Originally the Oak-Chestnut forest occupied areas assigned to Haven loam, Plymouth fine sandy loam, and Plymouth loamy sand, Sassafras fine sandy loam and Sassafras loam. The approximate correspondence between soils and vegetation of the Hempstead Plains (grasslands) is such as to suggest either inaccuracies in the boundaries set by the surveys, or a very slow encroachment of one type of vegetation upon the property of another type. But the Oak-Pine (Pine Barrens) vegetation straddles several soil types, parts of which are occupied by deciduous forest. Thus there is no precise correlation between soil types and vegetation, except in the Littoral areas.

Mechanical analyses of Long Island soils were given in the Soil Survey of 1904 by Bonsteel et al. We quote freely (Table 2).

> The Alton Stony Loam (an Oakwood soil, now Haven loam and stony loam) consists of a medium to fine brown or reddish yellow sandy loam, having a depth of six inches to one foot. The subsoil is somewhat finer sandy loam, usually of a reddish tinge from the stain of hydrated iron salts. It extends to a depth of 30 inches or more, and is underlain by gray or yellow cross-bedded sand and gravel. Both soil and subsoil contain numerous glacial boulders of trap, granite, gneiss, quartzite, shale and conglomerate, and sandstone rock. The soil is also constantly gravelly. The gravel is well rounded to subangular white quartz or crystalline pebbles and often reaches 30% of the total soil mass. (p. 20).

TABLE 2

Mechanical analyses of Long Island Soils.
from Bonsteel et al. 1903.

No.	Description	Organic matter	Gravel 2-1 mm.	Sand, 1-0.5 mm.	Sand, 0.5-0.25 mm.	Sand, 0.25-0.1 mm.	Sand, 0.1-0.05 mm.	Silt, 0.05-0.005 mm.	Clay, 0.005-0.0001 mm.
	Mechanical analysis of Alton Stony Loam, p. 22								
8946	Brown sandy loam 0-5 in.	4.78	4.4	17.7	14.	13.5	10.6	26.9	12.2%
8942	Ditto 0-9 inches	1.25	3.7	18.	9.9	7.6	13.8	34.4	12.7%
8943	Red sandy loam subsoil of 8942 9-30 inches.	.74	4.7	15.5	10.1	7.	13.5	38.2	10.94%
	Norfolk coarse sandy loam, p. 27								
9006	Coarse yellow sandy loam, 0-6 in.	2.27	7.4	25.84	18.04	13.76	6.96	18.5	9.5%
9007	Coarse yellow sandy loam, subsoil of 9006 6 to 36 inches	.82	9.98	30.64	18.2	11.62	5.06	16.02	8.1%
	Hempstead loam, p. 14								
8957	Brown loam, 2m. n.e. of Hicksville, 0-10 inches.	8.26	2.7	8.06	3.96	4.88	8.96	49.2	22.2
8958	Subsoil of 8957, yellow, silty loam, 10-30 inches.	.62	1.3	5.3	3.7	4.8	15.24	42.2	27.5

The surface soil of the Norfolk coarse sandy loam (a Pine Barren soil, now Sassafras sandy loam) to a depth of 8 inches consists of a medium to fine sandy loam of a reddish yellow color, which contains a large amount of fine gravel from 1/4 inch to 2 inches in diameter. The soil is always prevailingly sandy, but in the localities where the sand is medium in texture it packs to form a somewhat loamy surface. The subsoil is a granular sandy loam, containing a considerable amount of gravel. This reaches its greatest proportion at a depth of 16 to 24 inches. Below this depth the underlying material is a medium to coarse orange sand only slightly gravelly (Bonsteel, p. 25).

The surface soil of the Hempstead loam (Hempstead Plains Andropogonetum) to a depth of 8 inches consists of a friable brown or black loam containing a small amount of white quartz gravel and locally becoming somewhat sandy. From 8 to 24 inches the subsoil consists of a heavy yellow to reddish-yellow silt loam, slightly gravelly. It is very uniformly underlain at a depth of about 24 inches by a bed of rounded quartz gravel embedded in a sandy loam matrix, all considerably stained by a coating of hydrated iron salts. (Bonsteel, p. 13).

In general, all of the soils except the marginal sands, and marsh and meadow mucks, are directly derived from glacial and cretaceous gravels. The upland soils are usually underlain by great depths of gravel. But occasional masses of cretaceous clay occur, making suspended water tables. If near the surface, these impermeable clays greatly affect the water supply for plants. At suitable depths they form sources of capillary water, or direct supplies for deep going roots. Closer to the surface they may cause seeping springs, or ponds without inlet or outlet—glacial kettles. The latter are usually stagnant, and show a great variety of vegetation and of hydrogen ion concentration. Probably they differ as much in dissolved nutrients.

Perahps it is these cretaceous clays that cause the great flow of cold spring water all along the base of the slopes on the west side of Cold Spring Harbor and the valley to the south. This enormous seepage has given the name to the harbor and village; it is the supply for the three ponds that once ran two mills, and was originally the water supply for the New York State Fish Hatchery. For many years, however, the hatchery has used artesian water, aerated by splashing into small tanks and runways. The water from the wells (about 100 ft. deep) is said to be more nearly pure H_2O than some samples of distilled water! The seepage of this cold water, together with north and east exposure, has made the habitat of our fragmentary Betuletum. On the A. Holdenpyl Estate at Locust Valley such seepage has been controlled for the development of an alpine garden, with sunny exposure and refrigerated subsoil.

Part II.—The Vegetation

Method of Investigation

The study of aquatic associations has been by inspection, and collection of material, with field notes of a general character. No measurements were made. In land associations, including *Spartinetum glabrae,* quadrats were laid out, and the plant covering counted, measured or estimated. Records were made on sheets ruled as in Fig. 3. In using this sheet a suitable stand is selected, the location, slope and visible soil conditions are noted, and a quadrat is laid out.

LF signifies life form. The letters in this column are already conventional: P, phanerophyte; Ch, chamaephyte; H, hemicryptophyte; Hy, hydrophyte; a, attached; ros, rosette; G, geophyte; r, rhizome; T, therophyte (annual).

LF	Name of Plant	Ab	CE	Vit	Per	Soc	Con	Remarks; Fid, Constancy, etc.

Fig. 3. Headings of record sheet used in field work. LF, life form; Ab, abundance; CE, combined estimate (cover); Vit, vitality; Soc, sociability (gregariousness); Con, constructiveness; Fid. fidelity. Cf. Braun-Blanquet, 1932.

In making association tables both in field and laboratory we have attempted to use the terms as defined by Braun-Blanquet (1932). The terms used in the table, Fig. 3, may be explained as follows.

Abundance, Ab, is an expression of the plentifulness of each species. The following scale is used:

1, very sparse (very rare)
2, sparse (rare)
3, not numerous (infrequent)
4, numerous (abundant)
5, very numerous (very abundant)

Combined estimate, CE (Total estimate of Braun-Blanquet 1932), is an expression combining the concepts of abundance and amount of space covered by the plants of each species. The scale follows:

+, sparsely or very sparsely present; cover very small
1, plentiful but of small cover value
2, very numerous, or covering 5 to 25% of the area
3, any number of individuals covering 25 to 50% of the area.
4, any number of individuals covering 50 to 75% of the area.
5, covering more than 75% of the area.

Vitality, Vit, is an expression of the vigor of the plants, especially with regard to capacity for reproduction. Discarding for typographical reasons the pictorial signs used by Braun-Blanquet, we have adopted a numerical scale:

1, occasionally germinating but not increasing; many ephemeral adventive plants.
2, feeble but spreading, never completing the life cycle
3, strong and increasing but usually not completing the life cycle.
4, well developed, regularly completing the life cycle.

Periodicity, Per, gives a record of the activities of the plant at the time the area was surveyed. The following signs are used:

fol, in leaf	fl, flowering
s. fol, leafless	fr, fruiting
b, buds	sdl, seedling

asm, assimilating (photosynthetic)

Sociability, Soc, has to do with the grouping (gregariousness) of the individual plants, according to the following scale:

1, growing one in a place, singly
2, grouped or tufted
3, in troops, small patches, or cushions
4, in small colonies, in extensive patches, or forming carpets.
5, in great crowds, (pure populations).

Constructiveness, Con, is an expression of the rôle of the plants of a species in the up-building, maintenance, or degradation of the community. Plants which maintain the association offer opposition to change, i.e., they tend to maintain the *status quo*. Again for typographical reasons, discarding the suggestive signs used by Braun-Blanquet, we have adopted a numerical code:

1, constructive
2, conserving
3, consolidating
4, neutral
5, destructive
23, conserving and consolidating
123, constructive, conserving and consolidating

Constancy, Cona, relates to the degree to which a species may be expected in a given association. It is expressed in a scale:

1, Constantly present (in 80 to 100% of the stands)
2, mostly present (in 60 to 80% of the stands)
3, often present (in 40 to 60% of the stands)
4, seldom present (in 20 to 40% of the stands)
5, rare (in 1 to 20% of the stands)

Fidelity expresses the extent to which a species is confined to a certain association. We recognize:

1, exclusive species: species confined, or almost confined to one association.
2, selective species; found most frequently in a certain community, but also, though rarely, in others.
3, preferential species: present in several communities more or less abundantly, but predominantly or with better vitality in one certain community.
4, indifferent species; without profound affinity for any community.
5, strange species: rare and accidental intruders from another community or relics of a preceding community.

The exclusive and selective species are obviously the most distinctive characteristics of the association.

In layered communities the number and boundaries of the layers are first ascertained. The height of the highest layer is measured, and a cover grade is assigned to the layer as a whole. The species are then listed and graded. Trees are counted and the circumference measured breast high. Each layer is similarly examined. Then the remaining portion of the stand adjacent to the quadrat is examined and any additional species recorded and graded. Differences in vitality or sociability are noted. Wherever possible, several different stands are examined. But not one association has been exhaustively studied for this general outline. The work of Johnson and York is the most complete ecologic study ever made of this vicinity. Only in the *Ulvetum,* the salt marsh association and the *Cakiletum* and *Ammophiletum* have fairly adequate numbers of stands been studied for the preparation of the lists of species herein. All of the other lists are little more than samples. Studies like that of Bharucha (1932) are much needed.

The Associations

Accepting the pronouncement of the Brussels Congress, we consider that the association is the fundamental unit of vegetation. The association is defined by its characteristic combination of species, i.e. the list of species and the rôle or function or place of the plants of each species in the community. A single concrete example of an association will be called a stand. A stand may be of any size, from a few centimeters across to many kilometers. It is not limited by its size, but only by the homogeneity of its vegetation. While the habitat is extremely important in the delimitation of associations, factors of the habitat are not essential in the recognition and definition of an association. The name and diagnosis are based upon the species list. In naming an association we have followed the custom of attaching the termination-*etum* to the root word of an important genus of the association. This noun is followed by the appropriate specific name in the genitive case, or by an adjective. For example, *Quercetum velutinae; Quercetum kalmietosum.*

On various occasions the association may be named by citing one or two important species, as *Chondrus-Ceramium rubrum* association; *Scirpus americanus* association.

There is a zonal distribution of vegetation in our area, the zones of which may be designated as formations.[4] First are the Maritime Formations along the salt waters of Long Island Sound and its bays, and of Great South Bay and of the Atlantic Ocean. Along the north shore above the influence of salt water is a deciduous forest formation. A narrow strip of deciduous forest borders the halophilous vegetation on the mainland along Great South Bay. Between these deciduous strips on the east half of our area is the Pine Barren formation, and on the west half the grassland formation of the Hempstead Plains (Fig. 1). The deciduous forest areas belong to the Oak-Chestnut forest formation of Shantz and Zon, the pine barrens to the Oak-Pine forest formation. The grasslands of the Hempstead Plains are floristically akin both to the tall grass prairie of central North America and to the border vegetation of the Pine Barrens between the trees and the mossland.[5] The associations of these zones will be characterized, and their sociological classification will be discussed.

1.—Maritime Formations

These associations are so clearly determined by the conditions of the habitat as to give the impression that they could well be named and classified thereby. They include plankton, benthic algae on stony bottoms, *Zosteretum* on silty sand bottoms, algae of shingle beaches, psammophytes and saltmarsh halophytes. They will be considered from the deepest water landward.

A.—Submersed Associations

1.—*Plankton*

The Ocean and Sound carry the populations of diatoms commonly found in such waters. The most abundant forms in Oyster Bay are *Chaetoceras* spp., occurring in very great numbers. No counts are available.

2.—*Laminarietum*

LF.	Species list	C.E.	Vit.	Soc.
Ha.	*Laminaria agardhii*	5.	4	5.
Ha.	*Chorda filum*	+	4	1.
Ha.	*Punctaria latifolia*	+	4	1.

Pure stands of *Laminaria*, fronds 2-3m. x 10-20cm., in dense beds on seaward (north) sides of large (over 2m.) rocks, attached to stones 2m. below the mean low water. Known at Eaton's Point. *L. agardhii* is very abundant

4 The combination of two ore more synusiae with uniform physiognomy and more or less uniform habitat requirements constitutes a "formation." The formation is entirely independent of floristic composition and may therefore, occur anywhere under similar external conditions. Braun-Blanquet 1932, p. 302.

5 Mossland is formed mainly by peat very poor in salts. Tansley, 1923, p. 59.

at the eastern end of Long Island (Montauk Point) along with *L. digitata* and *Rhodymenia palmata*. The fronds of *Laminaria* do not stand erect but spread out in every direction. They are often inhabited epiphytically by the hydroid, *Obelia geniculata*.

Fig. 4. Eaton's Point. Students holding a cluster of *Laminaria agardhii*, which grows just beyond the rocks farthest out. Lower right, rock covered with *Fucus*. Photo by H. B. Hornor, Aug. 1933.

Chorda filum attains a length of 1m. or more, occurring in clusters of 3 or 4, attached to a shell or small stone. *Ectocarpus siliculosus* occasionally occurs attached to *Chorda*.

Range: *Laminarietum agardhii* probably extends from Iceland to New Jersey (the range of the major species), though Farlow (1881) states that the Iceland plant is "doubtless true *L. saccharina*." Helgi Jonsson (fide Rübel, 1930, p. 302) recognized in Iceland distinct associations for *Chorda filum*, *Rhodymenia palmata*, and four species of *Laminaria*, six associations in all. Apparently the meager algal flora of Long Island is telescoped into fewer associations.

3.—*Chondrus-Ceramium rubrum Association*

Chrondus crispus (Ha) in tufts 5cm. tall, 6-10cm. in diameter, completely covers many rocks 0.4-2m. across, from a few cm. below mean low water to 1m. below. Apparently vigorous and completing the life cycle. A sub-association of *Chondrus* alone occurs on shingle (pebbles 4-10cm. in diameter) close to mean low water; the plants are about half size and apparently not completing the life cycle.

Ceramium rubrum (Ha) covers the tops of rocks about 30cm. below mean low water, the sides of the rocks being covered with *Chondrus*. Tufts are 3-10cm. tall, and apparently completing the life cycle.

Ulva lactuca (Ha) is often attached among the above red algae, and continues abundant to 30cm. above mean low water. The fronds reach 20-30cm. in length, apparently very vigorous. Among them sparsely is found:

Porphyra laciniata, 10-30cm. long, apparently healthy.

This association is best seen at Eaton's Point. It is also found on the rocky points to the north and northeast of Center Isalnd. *Laminaria agardhii* occurs as a "stranger" on stones in this association. The fronds are short (to 1m.) and narrow (to 10cm.), with greatly reduced vitality and pale color. The sub-association of *Chondrus* is seen at the west end of Cold Spring Harbor Sand Spit. Between the algae the rocks are covered with the barnacles *Balanus balanoides* and perhaps *B. eburneus.* At Montauk Point this association includes *Champia parvula* abundantly.

Range: New York to Iceland and Ireland, judging from the range of *Chondrus* and *Porphyra. Ceramium* and *Ulva* enjoy a worldwide distribution.

4. *Ahnfeldtia Association*

Ahnfeldtia plicata (Ha) occurs in tufts 10-20cm. long attached to pebbles or shells 2-5m. apart on silty sand bottom at 15cm. below mean low water. Eaton's Point.

Range: Unknown. The species is "very widely distributed in the colder parts of the North Temperate Zone" (Engler-Prantl I).

5. *Dasya-Grinnellia Association*

LF.	Species	C.E.	Vit.	Soc.
Ha.	*Dasya elegans*	+	4	1
Ha.	*Grinnellia americana*	+	4	1
Ha.	*Ceramium strictum*	+		1
Ha.	*Callithamnion* sp.	+		1
Ha.	*Lomentaria uncinata*	+		1
Ha.	*Champia parvula*	+		1
Ha.	*Griffithsia bornetiana* (not seen recently)			
Ha.	*Ulva latissima*	+	4	1

On sandy bottom on the east side of Center Island, these algae are found attached (except *Ulva)* to occasional pebbles or shells 10-50m. apart over a distance of half a kilometer. *Dasya* and *Grinnellia* are fruiting abundantly in August. *Ulva* floats loose on the bottom. The bottom here is 0.5-1m. below mean low water. It seems likely that these plants are more abundant in deeper water nearby, as numbers of them are washed up by storms. On this point we have no information. Occasional stalks and patches of *Zostera* formerly occurred on the sandy bottom of this region.

Range: This association is believed to extend from Cape Cod southward, since all of its species have that range. Unfortunately, southern limits are not available.

6. *Polysiphonia Association*

Ha *Polysiphonia variegata*
Ha *Bryopsis plumosa*
Ha *Graciliaria multipartita*
Ha *Ulva lactuca*

These species grow in great luxuriance attached to shells, pebbles or stones (up to 1m.) in a tide stream on the east side of Center Island. Although above the level of mean low water, they are never exposed to the air. For the stream carries a constant flow (very rapid at low tide) of salt water to and from a large salt marsh. Not enough fresh water enters from the island and marsh to dilute the water perceptibly; and there is no mud. The first two occupy a short portion of the stream (10m.) where it runs eastward. *Bryopsis* is on the north side or top of rocks which are shaded by the abrupt bank of the stream, therefore away from direct noonday sunlight.

Polysiphonia has been found on buoys and walls near the tip of the Cold Spring Harbor Sandspit, and *Bryopsis* is reported by Johnson and York from the east side of the Inner Harbor. The grouping of these species into an association may be purely local and accidental. But the group has persisted for more than twenty years.

In 1932 *Nassa obsoleta,* barnacles *(Balanus balanoides)* and starfish *(Asterias forbesi)* were noted in this association in the tide stream on Center Island.

The associations numbered 2 to 6 inclusive live in practically pure water of Long Island Sound. Davenport (1903, p. 157) says the water of the Sound has a specific gravity of 1.020, and that of Cold Spring Harbor outside of the Sandspit 1.019. Sea water of the North Atlantic measures about 1.022. All of the plants of these associations (except *Ulva latissima)* are *Hydrophyta adnata* (Braun-Blanquet, 1932, p. 290). Only in *Laminarietum* is there evidence of competition; in that association there is competition for space and light.

7. *Zosteretum marinae*

LF.		C.E.	Vit.	Soc.	Constr.	Fid.
H-.	*Zostera marina*	5	4	5	123	5

Occasionally epiphytic on *Zostera:*

Polysiphonia variegata
Ectocarpus siliculosus
Ceramium strictum.
Callithamnion Baileyi
Melosira granulata

Until the summer of 1932 this association covered many square miles in Great South Bay. It occupied brackish water 1-3m. deep, on silty sand bottom, with low, slow tides. Beside the algae named, it made a habitat for a number of animals as reported by Dr. Kornhauser's class in Great South Bay, July 14, 1931.

Crustacea: *Palaemonetes vulgaris, Virbius zostericola, Crangon vulgaris, Ovalipes ocellatus, Pagurus longicarpus, Panopeus sayi, Libinia marginata.*
Fishes: *Siphostoma fuscum, Opsamus tau.*
Snails: *Bittium nigrum, Littorina rudis, Cerithiopsis greeni, Nassa obsoleta, Urosalpinx cinereus, Acmaea testudinalis.*
Bryozoa: *Bugula turrita, Crisia eburnea.*
Tunicates: *Botryllus schlosseri, Molgula manhattensis.*
Isopod: *Idothea baltica.*
Annulate: *Lepidonotus squamatus.*
Hydroids: *Pennaria tiarella, Obelia dichotoma, Hydractinia echinata.*
Amphipods: *Carinogammarus mucronatus, Grubis compta, Amphithoe longimana, Caprella* sp.
Lamellibranch: *Mytilus edulis.*

According to Johnson & York, *Zostera* was formerly found in the Inner Harbor, Cold Spring Harbor, in patches 1000 feet in length, and of several hundred square yards area, with as many as 500 to 2000 leaf clusters per sq. yd. It commonly grew on muddy bottoms from mean low water to 3 ft. below this; extremes 1.5 to -4.5 ft. The lower limit was attributed to shifting of the bottom by currents in this vicinity. In Casco Bay, Maine, and in Great South Bay, Long Island, it grew at a depth of 10 ft. The upper limit was attributed to exposure to air, as *Zostera* cannot stand any desiccation Reference is made to Ostenfeld 1908.

There was formerly a stand of *Zosteretum* north of the Sandspit on sandy, silty bottom 30cm. below mean low water (Johnson & York, pp. 22-25).

There is intense competition among the plants of *Zostera* for space both in water and soil. The epiphytes have not been seen in large enough quantity to affect their host perceptibly.

In 1932 *Zostera* had completely disappeared along the Atlantic Coast of Europe and North America, where it extended from Iceland to France, and to New Brunswick and Florida. It has not returned (W. R. Taylor, 1933). A bacterial epidemic is the suggested cause for this disappearance. No other case is known of such a sudden elimination of an abundant species. It recalls the fate of the Passenger Pigeon, or the Flight of the Ttartar Tribes. With *Zostera* disappeared the various animals listed above as members of the community. A few specimens of *Zostera* were reported from North Carolina and from Great South Bay in 1933. A slight further development was reported in 1934.

8. *Ruppietum maritimae*

A narrow belt above the limit of *Zosteretum*, from mean low water to 1.25 ft. above that; extremes -0.5 to 1.5 ft. *Ruppia maritima* var. *rostrata* Agardh is usually in thin pure stands on fine muddy bottoms of the inner harbor, Cold Spring Harbor. Its location is determined by tide levels, requiring exposure to air from 0 to 4 hours daily. It flowers freely in July, August and September (cf. Johnson & York, p. 26). Since the disappearance of *Zostera*, it would be well to know whether *Ruppia* has spread over the area left bare. Unusual amounts of *Ruppia* were washed up along the shores by the Laboratory in 1934. Upon these plants *Ceramium botryocarpum* was frequent as an epiphyte.

Ruppia maritima is of worldwide distribution, living in brackish water, both marine and inland (cf. Setchell, 1924).

9. *Ulvetum latissimae*

(Fig. 5)

LF.		C.E.	Vit.	Soc.	Fid.	Constr.	Consta
Hn.	*Ulva lactuca latissima*	5	4	5	3	123	5
	Beggiatoa rosea	1	4	5		4	

This association appears as a green cover on muddy bottoms, or even on shingle (Oyster Bay) between mean low water and ⅔ of high tide, covering 5 to 400 sq. m. in one stand. It consists of more or less matted sheets (up to 1m. across) of *Ulva*. Under these sheets a pink film of *Beggiatoa* may often be found. Johnson & York (pp. 19-21) show that the large sheets of *Ulva* originate from zoospores which attach to shells, stones or leaves of *Zostera* along the channels of the Harbor. After reaching a size of 2-6dm., they break loose and continue their growth as free floating organisms. Large plants are scarce or wanting in April, but the small ones are very abundant. Disappearance of the large plants occurs between December and February. The extreme limits of *Ulva* are from -5 to +4 ft. Ratio of emergence to submergence at upper limit 1.17.

Fig. 5. *Ulvetum latissimae*, Inner Harbor. Students holding up large, perforated sheets of *Ulva*. Photo by H. B. Hornor, Aug. 1933.

Dr. S. Kornhauser reports (personally) that *Ulva latissima* is the home of the 2 snails, *Alectrion (Nassa) obsoleta*, and *Rissoa aculeata*, and of the sea anemone *Sagartia luciae*.

Davenport (1903, p. 158) says the specific gravity of the water of the Inner Harbor "varies from 1.018 near the entrance to 1.005 at the surface near the inlet of the creek."

This association may be treated as two-layered with competition for space between the individuals in each layer, but with *Ulva* providing an indispensable shield from the sun for *Beggiatoa*. *Nassa obsoleta* is a constant member of this community.

Range: Unknown, probably worldwide.

10. *Enteromorpha Association*

Where fresh water seeps or flows into a harbor, this association is always met. In the estuary at Cold Spring Harbor, *E. clathrata* lies in a solid mat 1-2cm. thick, densely interlaced, over several square meters in the furrows amongst *Spartina glabra*. Here it is exposed to air at every low tide. *E. intestinalis* occurs here only in the running water of the estuary, or in sluices that do not drain out, i.e., never exposed to air. Along the west side of the Harbor, *E. intestinalis* often forms dense beds 20-30cm. across where springs pour out fresh water, bathing it constantly at low tide. But it is fully exposed at low tide to light. At the southeast end of Oyster Bay a strong fresh water stream gushes over rocks which are covered with a mat of *E. clathrata* in parallel strands as much as 50cm. long. Wherever a pebbly beach has a seepage of fresh water above low tide, there is an abundance of *E. clathrata*, and in the stronger streamlets *E. intestinalis*. These algae therefore prefer an alteration of fresh and salt or brackish water, and *E. clathrata* withstands complete exposure to air. But they never occur above the reach of salt water, even in estuaries. Johnson & York (pp. 21-22) believe that the mats of *E. clathrata* along the margins and streamlets of *Spartinetum glabrae* are made up of plants broken loose from their attachments elsewhere.

Range: An *Enteromorpha intestinalis* association is recorded by Jonsson (1912) below the lowest *Fucus* zone in Iceland, and by Rübel in the same relation in Ireland. This arrangement of zones differs so completely from that on Long Island as to suggest a review of the identity of the species concerned, and of the habitat conditions of both. There can be no doubt of the essential relation of our *Enteromorphetum* to the flow of fresh water into the Harbor. "In fact [*E. intestinalis*] is almost entirely confined to parts of the shore near fresh-water streams" (Johnson & York, p. 55).

11. *Monostroma Association*

Monostroma latissimum (Ha) grows on small stones in the estuary at Cold Spring Harbor, at the upper limit of salt water, and above the range of *Enteromorpha*. It grows abundantly in tufts 1-2cm. tall and wide. No other macroscopic plant accompanies it (Cf. Johnson & York, p. 58).

B.—Zone-associations of Rocks and Walls

Where vegetation is assorted into distinct narrow zones, the groups may be advantageously considered together as zone-associations. On vertical walls which extend from low to high tide line, as at the Biological Laboratory, three distinct zones are found:

12. *Ascophyllum* zone-association.
13. *Fucus vesiculosus* zone-association.
14. *Rhizoclonium* zone-association.

On rocky shores made up of glacial boulders from 10 to 300cm. across the zones have a horizontal extension depending on the average slope of the shore. Johnson & York attributed the distribution of these zones to the differing abilities of the algae to endure exposure to air. Jonsson (1912) places this group in the "lichtliebende Unterstufe" of the "Littoralstufe," being above water at every ebb-tide.

The rockweeds increase in abundance as one goes northward. The zones become wider and more pronounced. Helgi Jonsson (*fide* Rübel, 1930, p. 302) recognizes in Iceland a *Fucaceae* belt with six sub-associations dominated respectively by *Pelvetia canaliculata, Fucus spiralis, F. vesiculosus, Ascophyllum nodosum, F. inflatus, F. serratus*. Rübel found similar associations in Norway, and *Fucus vesiculosus* in a belt directly above *Ascophyllum*. In Ireland he found *Fucus spiralis* just above *Ascophyllum*, and *F. vesiculosus* just below. This inversion of belts is not explained.

TABLE 3

Zone Associations of Rocks and Walls.

LF.		Ab.	C.E.	Soc.	Vit.
	12. Ascophyllum zone-association				
Ha.	*Ascophyllum nodosum*	5	4–5	4	4
	13. Fucus vesiculosus zone-association.				
Ha.	*Fucus vesiculosus*	5	5	4	4
Ha.	*Fucus evanescens*	1	+	1	4
Ha.	*Porphyra laciniata*	1	+	1	4
	14. Rhizoclonium zone-association.				
Ha.	*Rhizoclonium tortuosum*		4	5	4
Ha.	*Rhizoclonium riparium*		4	5	4
Ha.	*Enteromorpha crinita*		+	1	
	10. Enteromorpha zone-association.				
Ha.	*Enteromorpha clathrata*	5	5	5	4
Ha.	*Enteromorpha intestinalis*	5	+ to 5	2–5	4
	11. Monostroma zone-association.				
Ha.	*Monostroma latissimum*		+	3	4

12. *Ascophyllum Zone-association*

This alga hangs in dense fringes from vertical walls (Fig. 6) from 2 to 5 feet below mean high water, or sprawls on rocks at similar tide levels. Extreme limits at Cold Spring Harbor are —1 to +7 ft., the ratio of emergence to submergence being from 0 to 6 6 (Johnson & York, p. 158). The plants attain a length of 60cm.

Epiphytic on *Ascophyllum* are:

Melosira granulata	*Polysiphonia fastigiata*
Ceramium strictum	*Ectocarpus siliculosus.*

In clear water the rocks between the algae are occupied by barnacles *(Balanus balanoides), Nassa obsoleta, Modiolus demissus,* and starfish *(Asterias forbesi).* In Ireland the mussel of this association is *Mytilus edulis* (Rübel, 1930, p. 303).

Range: Iceland to Ireland and to New Jersey.

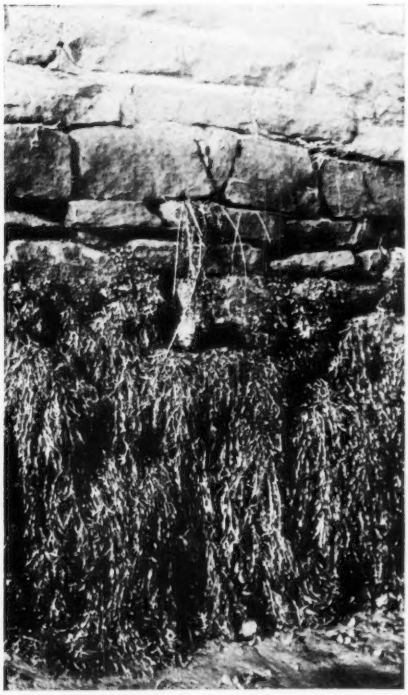

Fig. 6. Zone-associations on sea-wall at Laboratory. *Ascophyllum* below, *Fucus* above. The green zone of *Rhizoclonium* does not appear in the photograph. Photo by H. B. Hornor, Aug. 1933.

13. *Fucus vesiculosus Zone-association*

The Fucuses occupy a zone directly above and in contact with the *Ascophyllum* zone (Fig. 6). On a vertical wall of loosely laid sandstone at the Laboratory this zone is about 30cm. wide; on a vertical wall of cemented granite masonry at the northwest margin of Huntington Harbor 120cm. The first wall faces a little south of east; the second faces north and gets much less direct sunlight. *Littorina rudis, L. litorea, L. palliata,* barnacles and star-

fish are found among the algae. Extreme limits of *Fucus vesiculosus* are 0 to 7.25 ft., e:s ratio 0.08 to 11.45.

Range: Iceland to Ireland and to North Carolina. A *Fucus vesiculosus* zone with large patches of *Enteromorpha compressa* is shown in Pl. 3 of Massart's atlas of littoral vegetation of Nieuport, Belgium.

14. *Rhizoclonium* Zone-association

These algae make a green strip 10-20cm. wide directly above the Fucus zone on the wall at the Laboratory. They were not present as a zone on the wall at Huntington Harbor. The fine green threads are firmly pressed against the rocks at low tide. Indeed they are wet with salt water for only an hour or so at each tide.

On some wharves a band of *Rhizoclonium* 0.5 to 0.7 foot high is found above the rockweeds. This band, which often includes some matted *Lyngbya* and *Calothrix*, is frequently interrupted and not prominent when viewed from any great distance. (Johnson & York, p. 65).

Range: Unknown.

Marine algae not assigned to an association

1. *Hildenbrantia rosea* forms red blotches on quartz pebbles near mean low water, just above the level of *Chondrus*. It withstands exposure to air. It is found on the outer side of the Sandspit, Eaton's Point, etc.

2. *Sargassum* sp. Washed ashore at Eaton's Point, and sometimes taken in dredges near that point.

C. The Saltmarsh Associations

Where water currents in harbors and bays permit the deposition of silt, and the movement of water is slight, a muddy bottom is found. All gradations in the mixture of sand and silt or pebbles and silt occur. And wherever silt is deposited, there appears above the 5 ft. tide level the saltmarsh vegetation. Where there is a very gently sloping land surface the following zone-associations are found:

1. *Spartinetum glabrae:* 5-7 ft. tide levels.
2. *Salicornietum:* 7-7.5 ft. tide levels.
3. *Distichlidetum:* 7-8 ft. tide levels
4. *Spartinetum patentis:* 7.5-8 ft. tide levels.
5. *Scirpus americanus* association: 8-8.5 ft. tide level.
6. *Suaedetum* on still beaches of pebbles and silt: 7.5-8 ft.
7. *Spergularia* association, where *Spartinetum patentis* has been killed by piles of drift and the bare ground uncovered again, or where sand or gravel has been placed at the level of this Spartinetum.

On steeply sloping beaches there is less sand than pebbles, as on the south side of the Sandspit. Here only zones 1, 2 and 6 occur, in direct sequence. At many places zone 1 occurs, in stands from 1m. to many meters in extent.

The levels at which these zones occur are attributed by Johnson & York to the ability of the plants to endure immersion in salt water.

The saltmarshes and strands of Europe and North America are dominated by identical life forms. Some of the species are identical. Others are distinguished only by minute and technical differences which have but recently been recognized, or reckoned of specific importance. Massart's (1908) sumptuous plates of the associations at Nieuport, Belgium, might well have been made on Long Island! Compare especially Pl. 2, Fucus zone; 5, *Ammophila arenaria;* 23, *Cakile maritima;* 48, *Salicornia herbacea* and *Suaeda maritima;* 49, Limonium.

15. *Spartinetum glabrae*

Summarized list of species

LF.		Ab.	C.E.	Vit.	Soc.	Fid.	Cona
G.	*Spartina glabra alterniflora*	5	4	4	5	5	5
G.	*Lilaeopsis lineata*	1	+	4	4–5	5	5
G.	*Scirpus nanus*	1	+	4	5	4	4
H.	*Ascophyllum nodosum* var.	0–5	0–5	1	1	1	3
H.	*Fucus spiralis*	0–5	0–5	4	1	1	3

Species list for *Spartinetum glabrae*, by localities.

LF.	In each column the first figure is for C.E., the second for Vit.	Cold Spring Harbor Saltmarsh	Oyster Bay, s.e.	Oyster Bay, wharf	Cold Spring Harbor Sandspit
rG.	*Spartina glabra alterniflora*	4:5	4:5	4:5	4:5
rG.	*Lilaeopsis lineata*	+:4			
rG.	*Scirpus nanus*	+:5		+:5	
Ha.	*Ascophyllum nodosum* var.	5:1			
Ha.	*Fucus spiralis*		5:1		4:1

Accompanying species, according to Johnson & York:

Diatoms: *Melosira* sp., *Pleurosigma angulatum.*

Chlorophyceae: *Chaetomorpha aera, f., Cladophora expansa?, Enteromorpha clathrata, E. crinita, E. intestinalis, Monostroma latissimum, Ilea fulvescens, Rhizoclonium riparium, R. tortuosum, Vaucheria thureti?*

Myxophyceae: *Anabaena torulosa, Lynbya aestuarii, L. semiplena, Microcoleus chthonoplastes, M. tenerrimus, Oscillatoria limosa, Chroococcus turgidus* (rare), *Isactis plana, Rivularia atra, Spirulina tenuissima, S.* spp.

This association appears as a dense meadow of tall (1-2.5mm.) stout (1cm. thick) grass, with leaves 1cm. wide. It is the marginal emergent vegetation on muddy shores, where the soil is twice a day covered with salt or brackish water (Fig. 7). It grows to greatest height (and flowers freely in

August) between the 6 and 7 foot tide levels. Above this it either stops abruptly, or extends in shorter and weaker sods, growing only to a height of 10-20cm. At lower tide levels it is also shorter and does not flower. Large areas, therefore, do not flower at all. This dense canebrake carries from 270 to 600 (Johnson & York) or 653 (1934 class) stalks per sq. m. Over large areas there is no other macroscopic plant. Usually, however, the mud between the grass stems is dotted or densely covered with *Fucus spiralis*, or with a short, much branched, slender form of *Ascophyllum nodosum*. At the upper

Fig. 7. Small saltmarsh at west end of Sandspit. Fore, *Distichlidetum;* next beyond, left, *Spartinetum patentis;* right, *Spartinetum glabrae;* middle left, a strip of beach with *Ammophiletum* above. Hill beyond village, *Quercetum*. Photo by Rev. C. G. Bifoss, Aug. 1934.

limit of *Spartina*, either within or just outside its border, is often found a dense sod (20-100cm. across) of *Scirpus nanus*, 3-5cm. tall. And very rarely is found just within the upper margin of Spartina a sod (20-60cm.) of *Lilaeopsis lineata*, about 3cm. tall, flowering and fruiting in July. One such sod has maintained itself with slight fluctuations for over 20 years.

Modiolus demissus, the fluted mussel, fills the mud between and under the grasses along the margin of channels, binding the soil so firmly as to prevent erosion. Channels surveyed in 1910 are almost unchanged in 1933. *Ascophyllum* and *Fucus* are often attached to the shells of *Modiolus*.

Johnson & York discussed at length (p. 38-52) the "*Spartina glabra* association." They attribute the lower limit of the species (+1.5 ft.) to the long period of submergence, preventing air from reaching the rhizomes and roots. Upper limits (+6.5 ft.) are in general due to competition with other angiosperms for soil and light. And wherever there is any considerable flow of fresh water, *Spartina glabra* is absent.

Range: *Spartinetum glabrae* is described for the Bay of Fundy, N.S., by Ganong (1903), at York in extreme southern Maine, and Cape Cod, Mass. It occurs all along both sides of Long Island in suitable places, and along the bays of New Jersey. Shreve *et al.* (1910) recognized it in Maryland,

Kearney in North Caroilna, and Penfound and O'Neill (1934) on Cat Island, Miss. Presumably this is the *Spartina* which Lloyd and Tracy found in the Mississippi Delta. "In swampy ground of the lower levels which border on the salt water, *Spartina* gives the character to the vegetation, and this is often the sole plant." According to Rübel (1930, p. 292) on the coast of Hampshire (England) *S. stricta, S. alterniflora* and *S. Townsendii* (cf. Huskins, 1931) are dominant over wide areas, forming thickly matted sods into which scarcely any other plant can penetrate. *S. glabra* is attributed also to the Bay of Biscay.

Lilaeopsis occurs in eastern North America on the coast from New Hampshire to Florida and Mississippi. But it is also found in Australia, Tasmania, New Zealand, the Andes of South America, and from California to British Columbia.

Scirpus nanus frequents all of the seacoasts of the Northern Hemisphere.

16. *Salicornietum ambiguae*

Summarized list of species:

LF.		Ab.	C.E.	Vit.	Soc.	Fid.	Consta.	
Ch.	*Salicornia ambigua*	5	5	4	5	5	5	
T.	*Salicornia europaea*	1	+	3	1	1	1	Ruderal halophyte
H.	*Limonium carolinianum*	2		4	1	2	2	Pioneer of next zone?
rG.	*Distichlis spicata*	2	1	2	2	1	1	Pioneer of next zone.
T.	*Suaeda maritima*	1	+	4	1	1	1	Ruderal halophyte

Salicornietum on the Sandspit.

One meter quadrat

LF.		Ab.	C.E.	Soc.	Vit.	Constr.	Fid.	Consta.
T.	*Salicornia europaea*	5	5	4	4	123	4	5
H.	*Limonium carolinianum*	2	1	1	4	3	3	3
rG.	*Spartina glabra*	3	2	2	3	5	1	3
T.	*Suaeda maritima*	2	+	1	2	3	3	4
	10 meter quadrat, including the one, adds							
T.	*Atriplex patula hastata*	1	+	1	3	3	3	3
G.	*Spartina patens*	1	+	2	3	5	3	5
G.	*Solidago sempervirens*	1	+	1	3	3	2	4
	Outside the quadrats							
T.	*Atriplex arenaria*	1	+	1	3	3	2	3
Ch.	*Salicornia ambigua*	2	+	2	4	3	3	
G.	*Spartina patens juncea*	1	1	4	4			

On very broad saltmarshes with very gentle slope, as southeast of Bayville and at the west end of Lloyd Harbor, *S. ambigua* forms dense, almost exclusive beds 1-6m. wide and many meters long. The plant is about 30cm. tall, and flowers in August and September.

S. europaea is a kind of ruderal halophyte, springing up on any denuded portion of the saltmarsh from the 6.5 ft. tide level up to the limit of the high tides. From 7 to 7.5 ft. it flowers and fruits in abundance in exposed places. At higher levels it is often nearly devoured by insects, or crowded out by other plants. At the west end of Lloyd Harbor in 1933 it formed a dense undergrowth under *Iva oraria*. Usually it is marginal to *Spartinetum glabrae* (Fig. 8) and *Suaedetum maritimae*. About the Laboratory one could hardly speak of a *Salicorietum ambiguae;* the plant appears only occasionally at its appropriate tide level.

Fig. 8. Protected beach of Sandspit. *Spartinetum glabrae* on right, with a mixed stand of *Spartina patens*, *Salicornia* spp., *Suaeda* and *Limonium* reaching to middle. Dark spots on beach are *Suaedetum*. On left, *Ammophiletum*, with *Solidago sempervirens*. Photo by Rev. C. G. Bifoss, Aug. 1934.

Limonium may be scattered in the *Salicornietum*, or may form dense strips on the margins. It is equally at home in the next association. Perhaps it should be attributed to an association of its own. Ganong (1903) found a distinct *Limonietum ("Staticetum")* in the Bay of Fundy saltmarshes.

Range: Rübel (1930, p. 292) records *"Salicornietum herbaceae"* on the English coasts. *S. europaea* extends in North America from New Brunswick to Georgia, across the continent in wet saline soils, and on the Pacific coast; also Europe and Asia. *S. ambigua* is strictly American, "Mass. to Fla.; also Pacific coast" (Gray Man.) *Limonium carolinianum* occurs from Labrador to Texas (Gray Man.). Thus our *Salicornietum* must be confined to the middle Atlantic coast.

17. *Distichlidetum spicatae*

LF.		Ab.	C.E.	Vit.	Soc.
rG.	*Distichlis spicata*	5	5	4	5
H.	*Limonium carolinianum*	1	+	4	1
T.	*Salicornia europaea*	1	+	3	1
T.	*Suaeda maritima*	1	+	3	1

A difference in level of 2 or 3cm. at the 7 ft. tide level will favor *Distichlis* below and *Spartina patens* above (Fig. 7). Very often the patches of *Distichlis* appear to have taken possession of areas denuded by masses of drift (stalks of *Sp. glabra)* washed in by storm tides. *Spartina patens* is killed by such masses. A subsequent storm washes away the decayed remnants of the cover leaving a denuded area. If the sod itself rots away, a depression results, in which salt water remains after spring tides. Evaporation concentrates this, until conditions are unfit for any higher plants; the sod rots more, and a "tide pool" results. Such pools, 10cm. deep, remain for 20 years or more unchanged (Conard and Galligar). When filled with earth or gravel, *Distichlis* quickly runs its rhizomes across in interlacing straight lines and soon fills the area. *Spartina patens* and *Juncus gerardi* on the margins encroach very slowly, but will finally displace *Distichlis* at their own tide level. *Triglochin maritimum* was formerly found around some of the tide pools at Cold Spring Harbor.

On large saltmarshes there are large (20m) areas of pure *Distichlis*, 30cm. tall, and flowering freely in August. It stands adjacent to *Spartinetum glabrae* or *Salicornietum ambiguae*.

Limonium occurs in patches (Bayville; Lloyd Harbor) or as isolated plants.

Range: *D. spicata* occurs along the eastern coast from Nova Scotia to Texas, and this may be taken, provisionally, as the range of the association. Lloyd & Tracy (1901, p. 77) state that the *Spartina* spp. "in many places are largely replaced by Distichlis" in the saltmarshes of Mississippi and Louisiana. Penfound and O'Neill report a "Distichlis Consocies" on Cat Island, Miss.

18. *Spartinetum patentis*

LF.		Ab.	C.E.	Vit.	Soc.	Constructiveness	
rG.	*Spartina patens*	5	5	4	5	123	
rG.	*Juncus gerardi*	3	3	4	5	23	
H.	*Limonium carolinianum*	1	+	4	1	4	
rG.	*Distichlis spicata*	1	+	3	3	5	leading toward Distichlidetum
P.	*Iva oraria*	1	+	3	1	5	leading toward a shrub assoc.
T.	*Pluchea camphorata*	1	+	4	1	4	

This association covers areas from less than one sq. m. to many hectares or even kilometers in extent. The ground is perfectly level, and the dense fine grasses and rushes maintain an extremely even height. One sees apparently endless velvety stretches of yellow-green where low islands crowd together, or long strips of the mainland are broken only by narrow tide streams.

The yellow-green meadows of *Spartina patens* bear large brownish spots of fruiting heads in August, or similar spots of fruiting *Juncus gerardi*. The exact location of the *Juncus* beds remains exceedingly constant for as long as 20 years (Conard & Galligar). A *Spartina* sod bears about 1400 stalks per sq. ft. (Johnson & York). Wherever a few square centimeters of bare ground appear, *Distichlis spicata* is mixed, or establishes a pure stand.

Spartina, Juncus and *Distichlis* grow about 30cm. tall. By midsummer the stems fall over in various directions, making big shallows separated by ridges, like gigantic cow-licks (Fig. 7).

This association extends from the tide level of 6.5 ft. to 8 ft.; extremes 5.5 to 9 ft. Since mean high tide is 7 ft., there are long periods when much of *Spartinetum patentis* is not submerged. In other places it endures a brief daily submergence in sea water. The soil is a fine peaty silt, varying from 10cm. to 1 or 2m. in depth, densely matted with roots and rhizomes. At the latter depth we get the effects of a "quaking bog."

Range: This *Spartinetum* was described by Ganong for the Bay of Fundy (1903). It covers many level islands in Great South Bay, Long Island. It extends for many miles along the shores and islands of the inlets and bays of New Jersey, where the vegetation is cut and used as "salt hay" for bedding horses and for packing glassware. It is decorated in autumn by patches of *Sabbatia stellaris, S. gracilis* and *S. dodecandra,* and by marginal clumps of *Limonium carolinianum* and *Solidago sempervirens.* In Virginia and North Carolina this association forms "The Marshes of Glynn" that inspired Sidney Lanier. It is unmistakably indicated for Mississippi and Louisiana by Lloyd & Tracy (1901), and by Penfound and O'Neill (1934).

Ganong (1903) found a different relation of the plants and zones at the Bay of Fundy. His *"Spartina juncea"* forms an abundant *Spartinetum* of high marsh, with patches of *Glyceria maritima.* His *Staticetum* (with *Glyceria)* displaces *Salicornietum* and then engages *Spartinetum,* the two associations mingling to some extent.

Rübel records an upper saltmeadow belt dominated in England by *Juncus maritimus,* in Jutland by *J. Gerardi.* The next lower belt is *Glycerietum maritimae,* with *Limonium vulgare, Suaeda maritima, Triglochin maritimum Spergularia salina,* et al. The kinship of the European and North American associations is obvious. Braun-Blanquet records for Languedoc a *"Juncus Gerardi-Triglochin maritimum* association," as a member of his *Juncion maritimi.*

19. *Spergularia-Plantago decipiens Association*

LF.		Ab.	C.E.	Vit.	Soc.
T.	*Spergularia marina*	1–3	2	4	2
H.	*Plantago decipiens*	1–4	2–4	4	4
T.	*Gerardia maritima*		+	4	4
T.	*Pluchea camphorata*		+	4	2

On denuded spots in *Spartinetum patentis,* or on its border, or on artificially made sandy spots (filling up of tide pools for control of mosquitoes), *Spergularia* immediately appears in open stands. *Plantago decipiens* sometimes forms dense pure stands; usually it is scattered. It may be found fruiting abundantly on sand that is submerged only by storm tides, or it may flower and fruit where it is submerged twice a day. Perhaps *Triglochin maritimum* should be assigned to this very indefinite association.

20. *Suaedetum maritimae*

LF.		Ab.	C.E.	Vit.	Soc.	Constr.
T.	*Suaeda maritima*	4	2–3	4	2	23
T.	*Sueda* sp.6	4	1–2	4	2	23
T.	*Salicornia europaea*	1	+	4–1	1	4

A steep beach above the 7.5 ft. tide level, even in quiet bays, is torn by waves, ice and drift, especially in winter. The substratum is coarse sand and fine pebbles, with more or less of silt. Such a zone, in well protected places, supports in summer the *Suaedetum*. The glaucous-green semi-succulent linear leaves and red-purple stems of *Suaeda maritima* give a distinct color to this zone (Fig. 8). The plants are often 50cm. apart in pure stands, and 30-75cm. tall, rather columnar in outilne. Flowers and fruits are in September. At the lower margin of this *Suaedetum, Salicornia* occurs in more or less abundance. Seedlings of *Limonium* and *Oenothera biennis* sometimes occur, but the latter never mature.

Range: On the south side of the Sandspit, and both east and west of Bayville this association is typically developed. See *Salicornietum*.

21. *Scirpus americanus Association*

LF.		Ab.	C.E.	Vit.	Soc.	
rG.	*Scirpus americanus*	2	1	4	2	constant
rG.	*Spartina patens*	3	2	1	3	constant
rG.	*Eleocharis olivacea*	1	+	3	1	constant, exclusive
rG.	*Carex tenera*	1	+	4	1	constant, exclusive
T.	*Lysimachia terrestris*	1	+	1	1	constant
T.	*Ptilimnium capillaceum*	1	+	4	1	constant exclusive
T.	*Pluchea camphorata*	1	+	4	1	constant
T.	*Erechtites hieracifolia*	1	+	4	1	constant fid. 3
T.	*Hypericum virginicum*	1	+	3	1	constant

Since *Sc. americanus* is about 1m. tall and *Sp. patens, E. olivaceus* and *C. tenera* less than 0.5m., this zone-association is very conspicuous. However, it is little more than a transition zone between the halophile and the non-halophile vegetation. The first four plants named on the list form a dense sod. *Eleocharis* and *Carex* are found only in this zone. But they are very sparsely scattered and do not form a definite layer or seasonal facies. The little group of exclusive species may warrant recognition of this zone as a distinct association. It has been studied in this vicinity only at Cold Spring Harbor.

6 A form with only two stamens.

D. Beach associations

22. *Cakiletum edentulae*

LF.		Ab.	C.E.	Vit.	Soc.	Fid.	Const.
T.	*Cakile edentula*	2	+	4	1	4–5	5
T.	*Xanthium echinatum*	1	+	3	1	4–5	5
T.	*Euphorbia polygonifolia*	1	+	4	1	4	3
T.	*Salsola kali*	1	+	4	1	3	3
Ch.	*Ammodenia peploides*	1	+	3	2	5	2
Ch.	*Artemisia stelleriana*	1	+	3	3	3	3

Association list of *Cakiletum edentulae*

		Sand-spit I		Ashar-oken Beach II		Eaton's Point III		Bay-ville IV		Fire Island V		Jone's Beach Meisel-Bach VI	
LF.		CE	Soc.	CE	Soc.	CE	Soc.	CE	Soc.	CE	Soc.	CE	Soc.
T.	*Cakile edentula*	1.1		1.1		1.1		1.1		1.1		+.1	
T.	*Xanthium echinatum*	+.1		+.1		+.1		+.1		+.1			
T.	*Euphorbia polygonifolia*	+.1						+.1		+.1			
T.	*Salsola kali*	+.1						+.1					
Ch.	*Ammodenia peploides*			+.3		+.3						+.3	
Ch.	*Artemisia stelleriana*	+.3		+.3		+.3		+.3				+.3	

On beaches exposed to Long Island Sound or the Ocean, i.e. to strong wave action, there is no visible vegetation below the reach of spring tides. Such beaches are Mobilideserta. So also are the white beach sands above tide level. But just above the reach of spring tides, and within the reach of heavy storms (8.5 to 10 ft.), the very open Cakile association occurs. The plants are separated by centimeters or even meters of bare sand. Mostly this zone is only 0.5-1m. wide. When any of these plants (excepting *Euphorbia* and *Artemisia)* is found in the adjacent *Ammophiletum*, other evidence always shows that waves have dashed in during the preceding winter. The corky indehiscent mericarps of the cruciferous *Cakile* are admirably adapted for distribution by water.

Range: All around Long Island and along the New Jersey coast. Reported by Snow (1902) for Delaware, and by Cowles (1899) and others on Lakes Erie and Michigan. Probably coextensive with the range of *Cakile edentula*. This species is represented on the coast of Europe by *C. maritima*. The association corresponds in position to the *Agropyretum* of European coasts, lacking the *Agropyron*, as noted in the next section.

Fig. 9. *Ammodenia (Arenaria; Honckeynia) peploides.* Eaton's Point.

23. *Ammophiletum breviligulatae*

Association list; Sandspit.

In each column the first figure is for combined estimate, the second for vitality.

rG	*Ammophila breviligulata*	2:3	
rG	*Lathyrus maritimus*	+:4	
H	*Elymus virginicus*	+:4	
H	*Cyperus Grayi*	+:4	
Preferential species			
H	*Solidago sempervirens*	+:4	
T	*Euphorbia polygonifolia*	+:4	
rG	*Asparagus officinalis*	+:4	
T	*Polygonella articulata*	+:4	
Companion species			
P	*Myrica carolinensis*	+:4	
P	*Rhus glabra*	+:4	
P	*Rhus toxicodendron*	+:4	
Ch	*Artemisia stelleriana*	+:4	
Hros	*Oenothera biennis*	+:4	
Hros	*Lactuca canadensis*	+:4	
Accidental species			
P	*Quercus* spp.	+:1	
P	*Robinia pseudo-acacia*	+:1	
P	*Ailanthus glandulosa*	+:1	
G	*Anaphalis margaritacea*	+:4	
T	*Mollugo verticillata*	+:4	
T	*Cakile edentula*	+:4	
T	*Strophostyles helvola*	+:4	
T	*Gnaphalium polycephalum*	+:4	
T	*Ambrosia artemisiifolia*	+:1	
T	*Xanthium echinatum*	+:4	

The *Ammophiletum* originates by the settlement of *A. breviligulata* upon fresh fine sea sand, above all but the most extreme storm tides. Usual and extreme lower limits of *Ammophila* on the Sandspit are 8.75 and 8 ft. (Johnson & York, p. 100). The long rhizomes of the grass march in straight lines

into unoccupied sands (Fig. 10) and interlace in older settlements. The 0.5-1m. tall leaves and flower stalks catch wind-blown sand and function in the building of dunes. On Fire Island the dunes reach a height of 20m.

The stand is very open, 50-228 stalks per sq. m. (Fig. 10). The leaves are few, about 0.8cm. wide, exposing the smooth lower side to the sky even when spread out. But at all times except during rain each leaf is rolled into a cylinder, with the lower side out, and the ridged and furrowed upper surface inside. By far the larger number of stalks grow singly, 2 together or 3 together (Fig. 11). The appearance is of a very open stand of coarse grass, extending over dune and valley and flat.

Fig. 10. *Ammophiletum breviligulatae*. Sandspit. Photo by H. B. Hornor, Aug. 1933.

Lathyrus sprawls amongst the grasses at wide intervals, often forming small dense patches (a few meters). It is gregarious but decidedly hypodisperse.

Solidago sempervirens makes dense dark green clumps taller than the grass, at intervals of 0.5 to several meters, especially near the seaward border of *Ammophila*. The usual extreme lower limits on the Sandspit are 8.5 and 7.75 ft. (Johnson & York, p. 100). Its dense heads of golden bloom come in September. Although apparently halophilous in its natural habitats, it grows well when transplanted into a garden.

Rhus toxicodendron is sometimes as numerous as *Ammophila*, and with a higher cover grade; but more commonly it appears as isolated stalks, or dense tangles 1-20m. across. It piles up upon itself in mounds a meter high, and destroys all other plants within reach. Apparently nothing grows within its shade.

Rhus glabra and *Myrica carolinensis* are pioneers of a shrub stage. While

they are destructive to every species of *Ammophiletum, Myrica* in particular is favorable for the growth of other shrubs and for trees (Cf. Blizzard, 1931).

Artemisia is distinctly a border plant, belonging as much to the *Cakiletum* as here. *Cakile* and *Xanthium* are strays from their own adjacent zone.

Ailanthus has slowly increased its holdings on the Sandspit. It appears on the seaward margin of the beach-grass association. A clump of small saplings mapped in 1910 now has two trunks 15cm. and 20cm. in diameter breast high. Already in 1910 these sheltered a growth of *Poa compressa.* But the persons using their shade for recreational purposes have reduced the sandy surface to a desert.

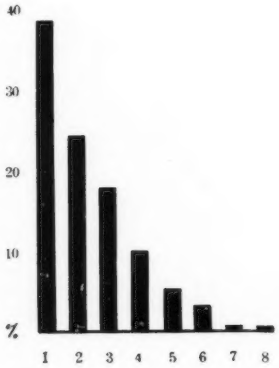

Fig. 11. Diagram of clustering of stalks of *Ammophila*, showing percent of stalks occurring singly (39%) and in groups of 2 to 8 (0.5%); from 3 quadrats.

The Habitat.—The soil of the *Ammophiletum* and *Cakiletum* was formerly listed as Galveston Sand. It is now mapped as Beach Sand and Dune Sand. It is made up mostly of particles of quartz. It is always grayish by reason of particles of black hornblende, and often reddish with garnet. It does not contain any notable amount of salt (NaCl). Benecke and Arnold (1931) found the limit of salt tolerance of *Ammophila arenaria* to be 1%. In all of the older grass-settlements the sand, beneath the surface, is darkened with humus.

Five cm. below the surface this soil is always moist. The xeromorphic characters of all the plants are not attributable to lack of available water. The illumination is very intense, due to direct sunshine, reflection from the sand, and diffuse light from the adjacent water. In spite of the sea-level atmosphere, the light of this habitat is as dazzling as the desert. Temperatures in the sun are high for the region, but are mostly tempered by cool breezes. Evaporation is not as intense as in a nearby seal-level garden; it is almost the same as in an upland garden (Transeau, cited under "climate"). Wind action is intense, often removing dunes and destroying the habitat. Thereupon settlement begins again. The sandblast action of the wind is marked. Pieces of glass left lying on the sand acquire a ground surface. Windows of adjacent

houses become "frosted," and it is difficult to keep the lenses of lighthouses in good condition, because of abrasion by wind-blown sand. Heat, light and wind may be regarded as the stimuli inducing xeromorphic structure in the *Ammophiletum* and *Cakiletum*.

Several types of xeromorphy are exhibited side by side:

Silvery-hairy covering: ---------- *Artemisia stelleriana.*
Hard, rolled leaves: ---------- *Ammophila breviligulata*
Heavy epidermis: ___ *Lathyrus, Xanthium, Solidago, Ammophila, Cyperus, Ammodenia.*
Succulence: ---------- *Cakile, Salsola, Ammodenia, Solidago.*
Reduced leaves: ---------- *Polygonella, Asparagus*

There is very little competition in the *Ammophiletum* amongst the members proper to the association, unless it be root-competition. *Solidago* is able to subdue adjacent grasses, but it is mostly widely scattered

The association must be considered as 3-layered: tall grass layer, ground layer *(Euphorbia)*, and root layer.

Range: Identical associations of *Cakile, Ammophila* and *Hudsonia tomentosa* have been observed by the writer in New Jersey at Lavalette, Atlantic City, Ocean City and Wildwood. Shreve et al. have described them for Maryland, and Harshberger for New Jersey and New England.

Snow has described on the coast of Delaware (p. 290) a "middle beach" "succulent zone" of *Cakile* sp., *Salsola kali, Xanthium* sp., *Atriplex arenaria.* Above this is a "low Ammophila dune zone" with *Ammophila* [*breviligulata*], *Panicum amarum, Euphorbia polygonifolia,* and *Oenothera humifusa.* One cannot be certain from her description just how the *Panicum* and *Oenothera* function in the community. Perhaps her association and ours are variants of one type. She also refers to *Hudsonietum.*

It is interesting to note that Cowles (1899, p. 116) describes on Lake Michigan a "middle beach" with "*Cakile americana* [*edentula*] dominant," along with *Corispermum hyssopifolium (Chenopodiaceae)* and *Euphorbia polygonifolia.* This association is very open, with plants far apart, as on the sea shore. On the "upper beach" (p. 168) occur *Lathyrus maritimus, E. polygonifolia, Oenothera biennis, Ammophila* [*breviligulata*], *Cakile* [*edentula*]. He adds (p. 177) "The most typical and successful of all dune-forming plants" along Lake Michigan is *Ammophila* [*breviligulata*]. The presence of these several maritime plants in the interior of the continent has been connected with the Champlain subsidence in post-glacial time, when salt water extended far inland, and extensive sandy beaches were continuous along the Great Lakes (i.e. their predecessors) and into central and western Wisconsin (McLaughlin, 1932).

The seashores of England, Belgium and France present almost identical conditions to ours. Tansley says (1923, p. 64) "The sandy seashore in front of the dunes, which is wetted only by the highest spring tides, is inhabited" by *Cakile maritima, Salsola kali,* [*Ammodenia*] *peploides, Atriplex* sp. and *Agropyron junceum.* "Just out of reach of the highest tides" *Ammophila arenaria* grows extensively and forms dunes.

On the Flemish coast Hocquette (Braun-Blanquet, 1932, p. 67) finds an *Agropyretum* consisting of *Agropyron junceum, Salsola kali* var. *polysarca, Atriplex laciniata, Cakile maritima,* [*Ammodenia*] *peploides*. The next zone contains *Euphorbia paralias, Ammophila arenaria, Elymus arenarius,* &c. Compare Massart's (1908) plates.

It should be noted that in Gray's Manual, Ed. 6, the common *Cakile* was given as *C. maritima,* and in Ed 7 *Ammophila arenaria* was still the accepted name for the American plant. The kinship of the associations on the two sides of the Atlantic is extremely close.

24. *Hudsonietum tomentosi*

(Fig. 12)

	C.E.	Vit.	Constr.
Hudsonia tomentosa	3-4	4	123
Lechea sp.	+	4	4

Hudsonietum presents areas 2-500m. across with more or less complete cover of the blackish stemmed and hoary-leaved shrub *Hudsonia,* 10-20cm. tall. Much of the soil is usually exposed, and practically nothing else grows within the area. Around the margins on Asharoken Beach, dying clumps of *Ammophila* are found. Whether they are injured by *Hudsonia,* or by the habitat conditions favorable to *Hudsonia* does not appear.

Fig. 12. *Hudsonietum tomentosi.* Asharoken Beach.

The soil is usually Beach Sand or Dune Sand. But near Fourth Lake, Cold Spring Harbor, there has long been a bed of *Hudsonia* 6m. across on a sandy abandoned railroad grade at the edge of oak woods. A similar bed is found on the sandy margin of a Sphagnum bog (an ancient lake shore) at

Lake Ronkonkoma. On Fire Island, at Montauk Point and elsewhere along the Long Island and New Jersey seashores, dune sand behind the dunes is abundantly occupied by this association. It appears to have occupied spots where the wind has blown away a dune—the sides of a "blowout," or the bottom of a shallow blowout. On Cape Ann, Mass., *Hudsonia* covers whole hillsides on shallow gravelly soil overlying granite rock.

The association is covered with a sheet of yellow bloom in May.

25. *Prunus maritima-Myrica carolinensis Association*

Behind the dunes of the Ocean front, and better back of the nearly level *Ammophiletum* of the shores of Long Island Sound, or the saltmarshes of Great South Bay, and the inlets and harbors of New Jersey, tall shrubs strike root in the fixed and humus-enriched sands: *Myrica carolinensis* 1-2m. tall. *Prunus maritima* 1-2m. tall.

These form dense tufts or beds two to several meters across dotting, crowding or covering the margin of *Ammophiletum*. They compleeely kill out the grass association. And in these habitats little else is able to survive. *Rhus toxicodendron* may come in and destroy. The association is still to be seen on Asharoken Beach, at Eaton's Point, and on the east side of Center Island.

26. *Juniperus virginiana Beach Association*

P *Juniperus virginiana*
S *Opuntia vulgaris* Mill. [= *O. compressa* (Salisb.) Macbride].

Mentioned by Transeau. Not studied. Asharoken Beach.

27. *Iva oraria-Baccharis halimifolia Association*

P *Iva oraria*
P *Baccharis halmifolia.*

At the margins of ditches in saltmarsh *(Spartinetum patentis)* Iva readily takes root, forming a half-shrub 1-1.5m. tall. It is also able to spread vigorously into *Spartinetum patentis* near the Laboratory. At the west end of Lloyd Harbor, *Iva* appears in dense stands at the inner (higher) side of the *Spartinetum*. Here it has a thick undergrowth of *Salicornia europaea* (in 1933). Only occasionally on Long Island is *Baccharis* associated with it, this 2-3m. tall shrub being uncommon here. In New Jersey *Baccharis* is much more common. The Long Island form of this association must be considered as imperfect or "fragmentary." Penfound and O'Neill (1934) report a similar association on Cat Island, Miss.

28. *Pinus rigida scrub association*

On Fire Island there is a dense mat of dwarfed pines 1-2m. tall about midway between the ocean and bay, on low ground. It is dwarfed and shorn off by the wind. Not studied.

29. *Vaccinietum macrocarpi*

Vaccinium macrocarpon
Bartonia virginica
Lycopodium sp.
Sabbatia stellaris
Aulocomnium palustre.

In the "dune complex,"[7] blowouts far behind the front line dunes often reach the level of ground water. These are covered with a thick growth of cranberry, fruiting abundantly. Among these and on the margins, the other plants occur in scattered fashion.

30. *Phragmitetum communis*

Phragmites grows 2-3m. tall, in dense sods 2-1000m. across, excluding everything else (Fig. 13). It is always found in very wet soils, often in standing water. The water may be brackish (Fire Island; Jersey City, N. J.) or perfectly fresh (Cold Spring Harbor). On Jones Beach the rhizomes form a coarse web on the surface of the ground for 10m. around the mature stands. In central Iowa it is in more or less calcareous water with continual flow or seepage.

Fig. 13. *Phragmitetum*, in rear; front, *Ammophila* invading bare sand; between, *Myrica* thicket. Dune complex, Fire Island.

The same association is described from south and central Europe (Rübel, 1930, p. 288). Probably it occurs wherever the species is found: "throughout North America, also in Europe and Asia," (Taylor, 1923, p. 135); "nearly throughout the United States, extending north to Nova Scotia, Manitoba and British Columbia. Also found in Europe and Asia, rarely ripening seed," (Britton and Brown, 1913, **1**: 232).

2. The Deciduous Forest Formation

As shown on the map (Fig. 1) the north and south sides of the mainland of Long Island, within the Maritime Formations, are covered with deciduous forest. This is chiefly composed of species of oak. Several well-defined associations take part, upon the moraines of the north part of the island. The

[7] The promiscuous mixture of associations behind and among and including the dunes (assoc. 22-24, 26-29) was called by Cowles (1899, p. 194) the dune complex, because it lacks zonation.

deciduous strip on the south side has not been studied, nor has the band around Lake Ronkonkoma. All of these associations show considerable ability to re-occupy abandoned land which they formerly occupied. This formation has been carefully described by Nichols for Connecticut. In our area we find:

31. *Quercus prinus* association.
32. *Quercus prinus* association with *Kalmia latifolia*.
33. *Quercus velutina* association.
34. *Liriodendron* association.
35. *Fraxinus—Juglans* association.
36. *Betula lenta* fragmentary association.
37. *Fagus grandifolia* fragmentary association.

Our area is near the limits of distribution of all of these associations. The oak, tulip tree and ash associations extend far to the south and west. Although the stands on Long Island are notably similar to those on the mainland of New York, in Connecticut, in southern Massachusetts, and about Philadelphia and Baltimore, in the absence of quantitative analyses in those regions, one cannot be certain of their identity. It is probable that south-eastern Pennsylvania and eastern Maryland will show more or less marked variants. Many other variants may be expected throughout the range of the Oak-Chestnut Forest of Shantz and Zon, to which associations 31 to 35 belong.

The *Betula* and *Fagus* associations are only fragmentary here. They are prominent in northwestern Connecticut, and from central Massachusetts northward. Long Island is therefore far outside their proper range.

31. *Quercetum prini*

Layers and species of a 10m. quadrat, with coverage (C E) and vitality.

Tall tree layer 5:

Quercus prinus	3:4	*Betula lenta*	1:4

Low tree layer +:

Acer rubrum	+:3		

Tall shrub layer 3:

Acer rubrum	+:3	*Viburnum acerifolium*	+:3
Cornus florida	+:3	*Castanea dentata*	+:1

Low shrub layer 2:

Azalea nudiflora	+:3	*Gaylussacia baccata*	+:2
Fraxinus americana sdl.	+:	*Prunus serotina*	+:
Quercus velutina sdl.	+:	*Vaccinium vacillans*	+:2

Ground layer

Aster divaricatus	+:3	*Deschampsia flexuosa*	1:4
Cornus florida	+:	*Luzula campestris*	+:3
Mitchella repens	+:3	*Chimaphila maculata*	+:4
Prunus serotina	+:	*Sericocarpus asteroides*	+:3
Smilax rotundifolia	+:	*Vaccinium pennsylvanicum*	+:3
Carya sp.	+:	*Epigaea repens*	+:2
Fraxinus americana	+:2	*Sassafras variifolium*	+:2

Moss layer (all spp. + :3-4)

Catharinea angustata	*Dicranella heteromalla*
Plagiothecium elegans	*Polytrichum ohioense*

This is a deciduous high-forest, with trees 30m. tall. Formerly with a copious admixture of *Castanea dentata,* this association was widespread and of great economic value. *Castanea* was a relatively rapidly growing hardwood, useful for fuel and fencing, and under a coppice or selection system, yielding a crop of lumber every 20 to 30 years. It sprouts vigorously from cut stumps. Its sudden destruction by the Chinese bark fungus *Endothia parasitica* furnishes one of the most striking examples known of the elimination of a species. As a result, the stands are at the present time more open than formerly in the upper layer, denser in the lower layers, and with more admixture of species strange to the association.

The association is three to five layered above the roots. There is competition for space and light within each layer, though the lowest layers are dependent on the upper for shelter from sun and wind.

The soil on the moraines is gravelly, with well developed humus layer, and 5-10cm. of leafy duff. The analysis of Alton Stony Loam is typical for the association. Where the soil is permanently moist this association quickly gives place to a *Liriodendretum, Fraxinetum* or *Aceretum* on peat. On cool north slopes *Betula* spp. and *Fagus* displace the oaks to a large extent, and a new herb layer appears.

According to Wherry (1923), *Rhododendron nudiflorum, Gaylussacia baccata* and *Vaccinium vacillans* prefer strongly acid soils; *Cornus florida, Betula lenta, Aster divaricatus* are indifferent: between neutral and sp. acidity 3 (pH 7-6.5). *Quercus prinus,* according to Weigand and Eames, grows on "dry neutral or acid, mostly rocky soil," p. 179. The Cayuga Flora attributes *Castanea dentata* and *Betula lenta* to "acid or neutral soils," *Acer rubrum* neutral or acid, *Cornus florida* mostly acid soil, *Viburnum acerifolium* acid, *Chimaphila maculata* "acid soil with chestnut and oak," Sassafras subacid soil, &c. Wherry further places the optimum acidity for *Azalea nudiflora,* and *Epigaea repens* at 30 sp. ac. (pH 5.54) of *Vaccinium pennsylvanicum* at 100 (pH 5). The discrepancies revealed in these figures indcate the difficulty in assigning plants to certain pH values. Plants belong rather to associations, in which they play a variety of rôles according to circumstances. Even more difficult would it be to assign a definite pH value to an association like *Quercetum prini.*

Range: If this association is characteristic of "Forest type 36, Chestnut Oak" of the Society of American Foresters (1932), it occurs in "Southern New England, New York except the Adirondack Mountains, Pennsylvania, New Jersey, and southward along mountain ranges at elevations of 1500 to 4000 ft. to Georgia and Alabama." Our own observations indicate that profound changes in the structure of the association take place in North Carolina.

32. *Quercetum kalmietosum*

Fig. 14

Layers and species of a 10m. quadrat, with covergrade (C E) and vitality.

Tall tree layer 3:4

Quercus prinus ---------- 3:4

Low tree layer 1:

Acer rubrum ---------- 1:3 *Betula lenta* ---------- :

Tall shrub layer 2:

Kalmia latifolia ---------- 2:4 *Quercus prinus* juv. ---------- 1:
Betula lenta juv. ---------- +:2 *Cornus florida* ---------- +:2
Castanea dentata ---------- +:1

Ground layer

Peramium pubescens ---------- 3: *Sassafras variifolium* ---------- +:1
Viburnum acerifolium ---------- +:2 *Nyssa sylvatica* ---------- +:1
Maianthemum canadense ---------- +:2

Moss layer (all spp. + :3-4)

Leucobryum glaucum
Hypnum imponens
Hynum recurvans
Hypnum reptile
Polytrichum ohioense
Plagiothecium elegans
Pohlia nutans
Dicranum flagellare
Dicranum scoparium
Dicranum montanum
Georgia pellucida
Dicranella heteromalla
Thuidium delicatulum
Bazzania trilobata

In general this association is similar to the preceding. It differs chiefly in the presence of *Kalmia*, giving a totally different physiognomy. There is less duff and more ground available for mosses. The remarks about *Querce-*

Fig. 14. *Quercetum kalmietosum* opposite Eugenics Record Office. About 1910, before *Castanea dentata* had been killed by *Endothia*.

tum prini apply as well here, as to height, former presence of *Castanea,* soil, and distribution.

Kalmia latifolia, Monotropa uniflora, and *Vaccinium corymbosum* are said to grow best on soil of 30 sp. ac. (pH 5.54). But this association is too dry for *Vaccinium* to prosper in it. *Maianthemum* and *Viburnum acerifolium* are assigned to strongly acid soil (Wherry). Cayuga Flora has *Cypripedium acaule* in acid humus on sandy or gravelly soils, and *Epipactus pubescens* on slightly acid humus. Braun-Blanquet has *Deschampsia flexuosa* when in quantity strictly confined to unsaturated humus soils. This seems more expressive than a figure for acidity. *Deschampsietum flexuosae* of Europe is a member of *Nardion* in *Caricetalia curvulae.*

33. *Quercetum velutinae*

Layers and species of a 10m. quadrat, with covergrade (C E) and vitality.

Low tree layer (30-50 ft.) 4:

Quercus velutina	3:4	*Quercus coccinea*	2:4

Tall shrub layer 1:

Kalmia latifolia	+:3	*Quercus prinus*	+:3
Quercus velutina	+:3		

Low shrub layer 4:

Gaylussacia baccata	3:4	*Vaccinium pennsylvanicum*	2:4
Quercus prinus	1:3	*Vaccinium vacillans*	2:4
Carya alba	+:3	*Kalmia latifolia*	+:
Quercus coccinea	+:	*Quercus marilandica*	+:
Quercus velutina	+:		

Ground layer

Deschampsia flexuosa	+:3	*Epigaea repens*	+:3
Baptisia tinctoria	+:2	*Carex* sp.	+:2
Prunus serotina	+:1	*Smilax rotundifolia*	+:1

Moss layer (all +:2-4)

Parmelia sp.	*Cladonia* (red fr.)
Dicranella heteromalla	*Cladonia* (brown fr.)
Dicranum scoparium	*Leucobryum glaucum*
Polytrichum ohioense	

Accessory Plants (outside the quadrat)

Betula populifolia	*Castanea dentata*
Gerardia pedicularia	*Helianthemum majus*
Pinus rigida	*Panicum* sp.
Quercus alba	*Cladonia* sp.

This is the dry oakwood, on southern slopes, or dry (over-drained) uplands. The three *Querceta* make up 90% of the deciduous forest formation throughout our area. The area is about equally divided between them.

Quercetum velutinae is a lower, thinner forest than the other *Querceta. Q. velutina* itself grows much larger when isolated, or in or between other associations, than in this association which it characterizes. We have been unable to assign it to any particular soil in the survey maps. Wiegand and Eames assign this oak to "light acid or neutral soils." This and *Q. coccinea*

"are good indicators of acid sandy soils." *Q. marilandica* is very markedly an indicator of dry sterile soils.

This association shows much similarity to the *Pinetum rigidae*. *P. rigida* often occurs sporadically in or near it. And many species are common to both associations. The soil and microclimate of *Q. velutinae* are intermediate between those of the other *Querceta* and that of *Pinetum*. *Pinetum* is bounded on the north by *Q. velutinae*, not by the other *Querceta*.

Range: This association agrees admirably with Forest "Type 33, Scarlet oak-black oak" (A.S.F., 1932, p. 20-21), which occurs on "Mountains and foothills of the Allegheny and Appalachian ranges, usually below 3,000 feet elevation, extending to the plateaus. Also in hill regions of Ohio, Indiana, Illinois and southward. Southeastern Missouri, but not Arkansas." This type is likely to be found throughout the botanical ranges of the two predominant species.

Dry ridges, south or west facing slopes and flats, but often extending to moister situations—.

Probably a climax type on the dry soils, giving way to chestnut oak in places.

There can be little doubt that the understories of this forest type are not uniform throughout its range, but data are lacking.

Cowles's (1899) "oak dunes," dominated by *Quercus velutina* have a flora similar to that of our *Q. velutinae*. Cowles lists 10 shrubs and small trees and 27 herbs on the oak dunes.

34. *Liriodendron Association*

Layers and species on a 10m. quadrat, with covergrade (C E) and vitality.

Tall tree layer 5:			
Liriodendron tulipifera	2:4	*Carya alba*	2:4
Low tree layer 4:			
Liriodendron tulipifera	2:	*Betula lenta*	1:3
Fraxinus americana	1:3	*Juglans cinerea*	1:3
Prunus avium	1:1		
Tall shrub layer 4:			
Benzoin aestivale	4:4	*Viburnum dentatum*	3:4
Liriodendron tulipifera	+:	*Carpinus caroliniana*	1:2
Cornus florida	+:2	*Sassafras variifolium*	+:1
Low shrub layer 4:			
Benzoin aestivale	2:	*Sassafras variifolium*	+:
Viburnum dentatum	1:	*Acer rubrum*	+:
Carpinus caroliniana	+:	*Fraxinus americana*	+:
Liriodendron tulipifera	+:	*Rhus toxicodendron*	+:1
Herb layer			
Agrimonia gryposepala	+:4	*Arisaema triphyllum*	+:4
Asplenium platyneuron	+:4	*Aster divaricatus*	+:3
Circaea lutetiana	+:4	*Epipactus pubescens*	+:3
Geranium maculatum	+:4	*Maianthemum canadense*	1:4
Prunella vulgaris	+:3	*Ranunculus recurvatus*	+:4
Trillium cernuum	+:4	*Veronica officinalis*	+:3
Rubus allegheniensis	+:1	*Actaea* sp.	+:2

Oxalis stricta	+:2	*Carex* sp.	+:1
Poa sp.	+:1	*Plantago rugelii*	+:2
Quercus velutina	+:1	*Rhus toxicodendron*	+:
Rubus triflorus	+:2	*Solidago caesia*	+:2
Vitis sp.	+:1		

Moss layer +:

Cirriphyllum boscii	+:1	*Brachythecium rutabulum*	+:1

Accessory species (outside the quadrat)

Fragaria virginiana	*Fraxinus americana* mature
Galium sp.	*Mitella diphylla*
Prenanthes alba	*Smilacina racemosa* +:4
Catharinea angustata	*Hypnum imponens*
Polyporus sp.	

The tallest, straightest tree trunks in eastern North America are those of *Liriodendron tulipifera*. Sometimes 2 or even 3m. in diameter, they tower to a height of 30 or 40m. In our area they occur in small patches, 50 to 100m. across, on moist slopes, associated with *Fraxinus americana, Juglans nigra, J. cinerea,* and *B. aestivale*. But the last two species are able to flourish on soil that is constantly full of seeping water, too wet for *Liriodendron*. On the mainland of New York near the city, *Liriodendron* is associated with *Benzoin* and *Carpinus caroliniana*. Near Philadelphia it is associated with *Benzoin* and *J. nigra*. Association lists are not available from these localities.

Range: Apparently a "fragment" of Type "53 Yellow Poplar" (SAF 1932), of the Appalachian Mountains and adjoining portions of the central forest, at altitudes of from 500 feet to 4,000 feet in the southern Appalachians, on moist lower slopes, northerly slopes, moist coves and flats, usually in small scattered stands.

35. *Fraxinus-Juglans Association*

Apparently such an association must be distinguished, since these trees reach mature size at a distance from any of those recorded above, especially on a moist substratum, with little competition from other trees. The exact relation has not been studied. This and the preceding association are related to Forest Type 49 White oak-black oak-red oak as developed in southeastern Pennsylvania. cf. Rübel's "Eschenwald," p. 153.

36. *Betula lenta Fragmentary Association*

Layers and species with covergrade (C E) and vitality, on a 10m. quadrat.

Low tree layer 5:

Betula lenta	4:4	*Acer rubrum*	1:3
Betula lutea	1:3		

Tall shrub layer 1:

Cornus florida	+:4	*Hamamelis virginiana*	+:3
Acer rubrum	+:	*Betula lenta*	+:

Low shrub layer 1:

Kalmia latifolia	1:1	*Acer rubrum*	+:
Fraxinus americana	+:	*Hamamelis virginiana*	+:
Smilax rotundifolia	+:1	*Vaccinium corymbosum*	+:1
Viburnum acerifolium	+:2	*Viburnum dentatum*	+:2

Herb layer 3:

Maianthemum canadense ---------- 2:4 *Aralia nudicaulis* ---------- +:3

Accessory plants (outside the quadrat)

Acer rubrum ----------	:3	*Arisaema triphyllum*	
Aster divaricatus		*Carex* sp.	
Carya sp.		*Geranium maculatum*	
Dennstaedtia punctilobula		*Kalmia latifolia*	
Juniperus virginiana		*Prunus serotina*	
Medeola virginica		*Quercus rubra*	
Quercus prinus		*Rubus triflorus*	
Quercus velutina		*Solidago caesia*	
Rhus toxicodendron		*Vaccinium pennsylvanicum*	
Smilax rotundifolia		*Catharinea angustata*	
Viburnum dentatum		*Dicranum flagellare*	
Dicranella heteromalla		*Hypnum reptile*	
Hypnum imponens		*Polytrichum ohioense*	
Leucobryum glaucum		*Platygyrium repens*	

Betula lenta is a common tree on cool slopes, but rarely does it form a pure stand of any considerable dimensions. A ten meter quadrat nearly covers a stand. Obviously it represents an association that is better developed elsewhere. Brief visits to Mass., Vt. and N. H. have convinced us of the truth of this conclusion. On High Hill, L. I., there lingers one white pine *(P. strobus)* above the *Betuletum*. *Betula lutea* is found frequently associated with *B. lenta*. On areas devoid of duff there are abundant mosses, of boreal aspect. But many of the mosses of the New England *Betuletum* are missing from Long Island: *Calliergon Schreberi, Hylocomium proliferum,* &c. Forest "Type 9 White Pine" (SAF 1932) to which our *Betuletum lentae* apparently belongs, as a fragmentary association, occurs "from southwestern Maine to east central Minnesota and along the Appalachian Mountains to northern Georgia."

37. *Fagus grandifolia Fragmentary Association*

The beech is found near to the Betulas, sometimes mixed with them. We have not found anywhere a stand made up largely of beech, nor any recognizable association of which beech is a part. Its relations are so fragmentary here as to be unrecognizable. *Epifagus* is common on the roots of beech.

3. Pine Barren Formation

This group of associations occupies a large rather flat area, with slight depressions to accommodate the shallow streams which flow rapidly over smooth sandy bottoms. Broad depressions are occupied by swamps of *Sphagnum* and low ericads, or with tall shrubs, or with stands of *Acer rubrum*. The uplands were originally covered with the forest of *Pinus rigida*. Nowhere have we found a dense stand of this species. Everywhere axe and fire have worked havoc. George Washington wrote in April, 1790, that the pine barren region of Coram, Long Island was "too poor to admit inhabitants or cultivation, being a low scrubbly oak, not more than two feet high, intermingled with small and ill-thriven pines" (Taylor, 1922). By far the greater part of

the Pine Barren is now occupied by scrub oak, often in almost impenetrable masses. The soil may be judged by the analysis of "Norfolk coarse sandy loam" (above). Low grounds are overlain by more or less depths of peat. A careful account of the Pine Barrens of L. I. was published by Roland Harper in 1908. The New Jersey Pine Barrens were described and discussed in a volume by J. W. Harshberger.

Range: The Pine Barren Formation of Long Island is continued northward upon Cape Cod, and southward through New Jersey, Delaware and Maryland. The several associations repeat themselves with surprising fidelity. Fernald (1933) has found very significant fragments on Newfoundland! He has suggested that the Pine Barren flora is ancient, and attained approximately its present distribution before the Pleistocene glaciation. Probably it wintered over the last glacial period on an off-shore land area now submerged. Since Fernald's proposal was made, it has been shown (Antevs) that the sea was 100 to 150 ft. shallower than at present when the ice had its maximum accumulation, and that isostatic compensation owing to the weight of the ice probably raised the portion of the earth's crust now submerged south of Long Island many feet farther from the center of the earth than it now is. Thus an extensive off-shore land area must have existed.

Transeau (1913) has counted the number of pine barren species that occur in relation to the great estuaries that break the area into separate parts. He says " of the 298 species of southeastern Virginia, 94 fail to cross the Chesapeake Bay. At Delaware Bay the list is decreased to 179 by the loss of 25 species. In Central New Jersey 15 drop out. At New York harbor the remaining group of 164 species is diminished by 45. Twenty-seven species reach their northern limit on Long Isalnd, and of the 92 which reach Massachusetts 55 go no farther. This leaves 37 to find their "farthest north" along the coast of Maine and the maritime provinces of Canada."

Whatever corrections these figures might require at preesnt, they will still remain significant. Transeau believes that "The arrangement of the coastal plain plants according to their northern-most stations brings out clearly the fact that the greatest barriers to the northward migration along the Atlantic coast are, or have been" the wide water-ways that divide the coast. His postulated "early post-glacial barrier" in central New Jersey is provided by the waterway that divided that state in two during the "Pensauken submergence," (Harshberger, 1911). However the validity of the Pensauken submergence has recently been seriously questioned (Lutz, 1934).

Transeau assumes a *northward* migration of plants to Long Island in post-glacial time, along the present land area. A shoreward migration from a land mass now submerged seems much more plausible. The estuaries might still account for the limitation of species, owing to the vast submergences signified by the Pensauken period.

Transeau's figures indicate that the Pine Barren associations are far from being identical in composition from Cape Cod to Virginia. Careful study might require the recognition of variant associations, and of some associations not represented on Long Island. For example, *Chamaecyparis* occurs on Long

Island in too small colonies to form an association. But in southern New Jersey a stand of *Chamaecyparetum* covers many acres.

Shantz and Zon characterize the Pine Barren regions as Oak-Pine forest, and this "forest" is continuous from Long Island to Georgia and Texas. The *Pinus rigida* association gives place to *P. taeda* associations in Maryland, and to *P. palustris* associations in North Carolina. Perhaps all of these associations should be classed as *Pinetalia,* in which *Pinion rigidae, Pinion (-etum) taedae* and *Pinion palustris* unite.

The Society of American Foresters include the Pine Barrens in their "Type 37 Pitch pine," which occurs from Northern New England, New York, Pennsylvania and New Jersey, southward along the Appalachian and Cumberland Mountains to Georgia, also in New Jersey on sands of the Coastal Plain. But the associations of the coastal plain will probably have a specific composition different from that of the mountain regions. Brief observations in the Pocono region of Pennsylvania indicate this.

The associations so far recognized are:

38. *Pinetum rigidae.*
39. *Quercetum ilicifoliae.*
40. *Aceretum osmundaceum.*
41. *Aceretum rubri.*
42. *Vaccinietum corymbosi.*
43. *Chamaedaphnetum calyculatae.*
44. *Chamaecyparetum thyoidis* (fragmentary).

38. *Pinetum rigidae*

Layers and species of a 10m. quadrat, with covergrade (C E) and vitality.

Low tree layer 3:

Pinus rigida	3:4

Low shrub layer 5:

Quercus illicifolia	4:4	*Gaylussacia baccata*	2:4
Quercus prinoides	2:4	*Smilax glauca*	1:4
Pteridium aquilinum	1:4	*Quercus alba*	+:2

Ground layer 3:

Vaccinium vacillans	3:4	*Gaylussacia baccata*	+:3

Accessory plants (outside the quadrat)

Gerardia pedicularia	+:4	*Myrica asplenifolia*	+:4
Baptisia tinctoria		*Lyonia mariana*	
Tephrosia virginiana		*Rhus toxicodendron*	
Carex sp.			

We have been unable to find *Pinetum rigidae* in approximately primitive condition anywhere on Long Island. South of Riverhead there is an area that should be examined. Nearly all of the Pine Barren is now covered with *Quercetum ilicifoliae,* both on Long Island and in New Jersey.

39. *Quercetum ilicifoliae*

Pinus rigida
Quercus prinoides
Gaylussacia baccata
Baptisia tinctoria
Lyonia mariana
Melampyrum lineare
Grass
Polytrichum commune
Russula sp.
Clavaria sp.
Arctostaphylos uva-ursi
Boletus sp.
Smilax glauca
Solidago bicolor
Quercus ilicifolia
Vaccinium vacillans
Gerardia pedicularia
Helianthemum majus
Myrica asplenifolia
Panicum sp.
Cladonia (red)
Mushrooms
Tephrosia virginiana
Quercus alba
Castanea dentata
Solidago odora
Pteridium aquilinum

This dwarf oak association covers many square miles on Long Island and in New Jersey with a dense, often impenetrable, thicket, 1-2m. tall. It is usually the result of fire, which destroys the pine. The few scrub oaks in the original forest sprout up abundantly from the uninjured roots and quickly mature a crop of acorns. Then a new generation arises and soon the whole terrain is occupied. Subsequent fires destroy the surviving pines, and the dwarf oaks sprout again, completely shading the soil and preventing any other trees or shrubs from getting a start.

In open places along roads or railways, or on very barren ridges, a number of characteristic plants appear, whose social relations we are not yet able to assign: *Sericocarpus asteroides, Hudsonia ericoides, Gaultheria procumbens, Liatris spicata,* &c.

Range: See above under Pine Barrens.

40. *Aceretum osmundaceum*

Along streams in broad flat valleys there is often a dense low thicket of *Acer rubrum,* 10-15m. tall. There is more or less of undergrowth. The shrubs are *Vaccinium corymbosum, Clethra alnifolia, Azalea viscosa.* Large clumps and beds of *Woodwardia areolata* and *Osmunda cinnamomea,* and frequent plants of *O. regalis* are found, and on sandy soil (not on peat) *Symplocarpus foetidus.* In a wetter, peaty phase, *Acer* is shorter and more scattered, the shrubs are larger and more numerous; *Sphagnum* covers the bases of the shrubs and the treacherous peat between, with *Drosera rotundifolia, Pallavicinia Lyellii,* and *Odontoschisma prostratum. Woodwardia virginica* and *Rhus vernix* enjoy such company. The wet *Aceretum* is also seen in the Pocono region of Pennsylvania. Association lists have not been made. West of Wyandanch station is an *Aceretum* with only *Osmunda cinnamomea,* in dense stands, as an understory.

Range: Unknown.

41. *Aceretum rubri*

Layers and species of a 10m. quadrat, with covergrade (C E) and vitality.

Low tree layer 5:
Acer rubrum ---------- 5:4

Shrub layer 1:

Clethra alnifolia	1:2	*Rubus* sp.	+:1
Vaccinium corybosum	+:2	*Benzoin aestivale*	+:2

Ground layer 2:

Rubus triflorus	1:3

This association occurs in peaty areas in the Deciduous Forest Formation, and belongs to it. It is inserted here because of its obvious relation to the richer and more varied *A. Osmundaceum*. At Woodbury bog, *Woodwardia virginica* was formerly found in the margin of the *Aceretum*. At Valley Stream the *Aceretum* is in the margin of a wood made up largely of *Liquidambar styraciflua*. Above III Lake, the *Aceretum* is on peaty soil which seems to have originated since the making of the lake, and because of the damming of the water.

Range: Unknown. No red maple forest type is recognized by SAF.

42. *Vaccinietum corymbosi*

Between *Pinetum* and *Aceretum* there is often a wide *Fruticetum* in which *Vaccinium corymbosum* is conspicuous. Such areas provide the highest quality blueberries for the market. This is the home of *Viburnum cassinoides, Rhus vernix, Osmunda cinnamomea, Woodwardia virginica, Sphagnum* sp., *Gaultheria procumbens, Polygala lutea, Habenaria blephariglottis, H. ciliaris, Drosera longifolia.* Association lists have not been prepared.

Range: Also in southern New Jersey.

43. *Chamaedaphnetum calyculatae*

Where *Sphagnum* overlies water, or soft watery peat, it soon is occupied by *Chamaedaphne*, so that a pure *Sphagnetum* cannot be said to exist in our region. Margins next to open water are usually occupied and actively extended by *Decodon verticillatus*, which steps out, stolon-wise, over the water by means of floats of spongy cortex. On the *Sphagnum* are *Drosera rotundifolia, D. longifolia.* In shallow places (1-5cm.) with constant water level *Eriocaulon septangulare* and *Xyris flexuosa* may abound. *Gratiola aurea* is common on wet sandy margins. *Eriophorum virginicum, Rhynchospora alba* and *R. glomerata* are to be expected. Ditches and still pools contain *Peltandra virginica, Pontederia cordata, Utricularia vulgaris, U. purpurea, U. minor?, Nuphar advena, Nymphaea odorata minor.*

Proper association lists have not been prepared.

This association often merges insensibly into *Vaccinietum*, and that into *Aceretum*. This fact, coupled with the fact that all are on a peaty substratum, proves that the three associations are continuous stages of a sere.

Range: *Chamaedaphnetum* is a characteristic sphagnum-bog association throughout the range of *C. calyculata*. "Lab. to B.C., s. to Minn., Wisc., Ill., and Ga. (Eurasia)" Gray Man., p. 636. (Cf. Nichols 1915, p. 199-201).

44. *Chamaecyparetum thyoidis*

The cedar swamp is a striking feature of the Pine Barrens of New Jersey and Maryland. On Long Island only fragments of the association appear. A

cluster of trees at Hauppaug is associated with *Viburnum cassinoides, Rhododendron viscosum, Clethra alnifolia,* and the mosses *Drepanocladus exannulatus* and *Calliergon cuspidatum.* This is the only record of this *Calliergon* on Long Island.

A *Chamaecyparetum* at Wantagh has not been studied and no association lists have been made. The stations for *Chamaecyparis thyoides* are shown on a map of Long Island by Taylor (1915a).

Range: Forest "Type 90 Southern white cedar. Characteristically in pure even-aged stands, although sometimes only predominating" occurs "in many detached tracts in Coastal Plain from southern Maine to northern Florida and southern Mississippi in a comparatively narrow zone near the coast. Most abundant in New Jersey, North and South Carolina and western Florida." (Cf. Korstian, 1924).

4. Grasslands

The natural grassland of the Hempstead Plains has been described in two papers by Roland Harper (1911, 1918). Grasslands at Montauk Point have bzeen described by Norman Taylor. The so-called grasslands of Shinnecock Hills are mostly occupied by cricads, in which the grasses have a minor rôle. Other "natural" grasslands occur as a stage in succession on abandoned land. But once established they are very resistant to change. Such a grassland was described by Blizzard on High Hill. Similar vegetation is found on many neglected fields and railroad banks, on Long Island, in Connecticut and Mass., and in eastern Pennsylvania. This study has to do with the

45. *Andropogonetum scoparii* of Blizzard, and the

46. *Andropogonetum Hempsteadi* of the Hempstead Plains.

45. *Andropogonetum scoparii*

Andropogon scoparius
Cladonia rangiferina
Polytrichum commune
Bryum caespiticium
Ceratodon purpureus
Hypericum gentianoides
Hypericum perforatum
Hieracium scabrum
Chrysanthemum leucanthemum
Sericocarpus asteroides
Juncus tenuis
Solidago rugosa
Rumex acetosella
Cladonia symphycarpa epiphylla
Polytrichum piliferum
Rubus villosus
Carex virescens
Stenophyllus capillaris
In old ashes of a camp fire
  Gnaphalium polycephalum
  Verbascum Thapsus
Juniperus virginiana
Seedlings of:
  Quercus velutina
  Quercus alba
  Robinia Pseudo-Acacia

Blizzard (1931) has shown that the area on High Hill is an abandoned pasture. It has remained almost unchanged since 1909, and doubtless for a long time before that. The large tussocks of grass are separated by as large, or larger, areas of gravelly sand (Fig. 15), densely covered with Cladonia, and sprinkled with *Polytrichum commune* and *P. piliferum.* Very slowly the deciduous forest is encroaching on the margins; and *Myrica carolinensis,* coming

Fig. 15. *Andropogonetum scoparii.* Columnar forms of *Juniperus virginiana* in background. High Hill.

up in the midst, kills the grass, and builds humus and duff in which oaks, maples and cherries are getting a start. *Juniperus virginiana* is scattered about, but not enough to greatly affect the association. Both *Juniperus* and *Andropogon* are being killed out by the encroachment of deciduous forest *(Quercetum prini* and *Q. velutinae).*

The ability of *Andropogon scoparius* to take possession of abandoned agricultural land or other denuded areas is conspicuous on Long Island, in Connecticut, Massachusetts and in southeastern Pennsylvania and perhaps elsewhere.

A railroad bank of sand and gravel, facing south ½ mi. east of Cold Spring station has clumps of *Andropogon* 0.5-1m. apart, with mostly pebbles between. Amongst these there is a small amount of *Polytrichum commune,* and a large amount of *P. piliferum.* In this small stand were also *Eupatorium hyssopifoium* (fl.), *Hypericum gentianoides* (fl.), *Lespedeza repens* (fl.), *L. virginica* (b.), *Lechea* sp., *Baptisia tinctoria* (1-2dm. across), *Helianthemum canadense* (fl.), *Cladonia symphycarpa epiphylla, C. rangiferina.* This closely simulates the conditions on High Hill. The stand has developed directly on bare sand and gravel. Such a development has been observed also near Woodbury.

In the lower ground to the south of the Drum Factory on a gentle slope facing north is a very dense and fine stand of *A. scoparius* covering several acres, all of it 40-50cm. tall, about to bloom (on Aug. 7, 1934). The cover-

grade of *Andropogon* is 5—certainly 90%—with only 5-15cm. between the clumps, and this mostly shaded and bare. There is very little *Cladonia* or *Polytrichum piliferum*. Under a small tree (2m. tall) *Polytrichum commune* and *Ditrichum tortile vaginans* were found. Scattered far apart in the grass were *Acerates viridiflora* (fr. juv.), *Helianthemum canadense* (fr.), *Lechea* sp., *Eupatorium hyssopifolium* (fl.), *Lespedeza capitata* (b.), *Juncus greenei* (1 stalk fr.), and sprouts of *Myrica asplenifolia, Betula populifolia, Quercus spp.*

All of these stands should be considered as phases of *Andropogonetum scoparii* of Blizzard. Cf. also Harper, 1920 (Alabama).

46. *Andropogonetum Hempsteadi*

This association in varied forms once covered the "Hempstead Plains" from Plainview on the east to Floral Park on the west, and from Hempstead on the south to the Jericho Pike north of Hicksville. This great stretch of natural prairie was considered unfit for cultivation until about 1915. Since that time much of the area has been plowed, and planted to truck crops. However, still (1934) large tracts, up to 100 acres, remain in essentially primeval condition showing in summer an expanse of yellow-green coarse bunch grass *(Andropogon scoparius)*, ½m. tall dotted thickly with ½m. hemispheres of *Baptisia tinctoria*. Gray shoots of *Helianthemum canadense, H. majus* and *Lechea* spp. are abundant. In special areas, not yet accounted for, *Juncus greenei* tints the prairie with its shiny castaneous capsules, or over many sq. m. *Scleria pauciflora* shows its tiny white bony achenes, or *Polygala sanguinea* appears, here a patch of red purple, yonder in the virescent phase. *Salix humilis* shares the honors with the doubly canescent *S. tristis*. In May the prairie is blue with *Viola lineariloba* and *V. fimbriatula*. In June ½m. tall wandlike stems of *Aletris farinosa* bear each a 10cm. cylinder of white bloom—about 1 to a square rod (Fig. 16). In late June *Baptisia* is full of yellow pea-shaped flowers and many clumps of the silvery *Tephrosia virginiana* show their heads of pink and yellow bloom. In July widely scattered stalks of the richly apricot colored *Habenaria ciliaris*, 3-5dm. tall dot the prairie. Late August brings bands and beds of red purple *Gerardia setacea*, 2-3dm. tall and countless stalks of the rich blue *Aster linariifolius* followed by acres of *A. ericoides, A. multiflorus* and *Solidago tenuifolia*. The continuity of the grasslands is broken by cushions 2 to 10m. across of *Quercus prinoides*. Other areas have *Lyonia mariana*, or *Gaylussacia baccata*. Occasional areas have *Quercus marilandica* in very open park-like formation. And feeble specimens occur—little more than sucker sprouts—of *Prunus serotina, Quercus stellata, Betula populifolia* and *Populus tremuloides*.

Andropogon furcatus occurs in scattered clumps, and *Sorghastrum nutans* and *Panicum virgatum*. All of these, together with *Viola pedata, Salix humilis* and *S. tristis*, and the dominant *A. scoparius*, are components of the tall grass prairie of Iowa and Nebraska, where *A. scoparius* is also dominant.

The Hempstead Plains have been carefully described in two papers by Roland Harper, where extensive lists of species may be found. The midwestern prairie has been recently described by Weaver et al. and by Steiger.

Fig. 16. Hempstead Plain in early July, 1928. *Aletris* spikes on left; *Baptisia* in front, behind the man. Maize field and trees in distance.

The similarity of the two communities is striking. They lie in the same floristic area (Region), which means that the same species are accessible to both. It appears that the extremely porous gravel of the Long Island grassland, bathed with a 48 inch rainfall, is ecologically equivalent to the fine wind-blown loess of Iowa and Nebraska with a 30 inch rainfall. Wind movement and evaporation are vastly greater in the middle west, and humidity much lower than on Long Island. In both areas, the plants have added large quantities of humus to the upper soil layers. The elevation of the Hempstead Plains is from 60 ft. above sea level on the south, to 140 ft. at the extreme northeast. The hundred ft. contour runs through the middle of the Plains.

A 3m. quadrat (9 sq. m.) in one stand gave the following conditions: Location of Quadrat: Southeast of Hicksville, on level ground. Aug. 29, 1933, by Helen Betty Hornor.

						Remarks
LF.	Name of Plant	C.E.	Vit.	Per.	Soc.	Constr.	Fid. const, etc.
H.	*Andropogon scoparius*	5	4	fr.	4	123	
P.	*Lyonia mariana*		3	fol.	1	4	
H.	*Baptisia tinctoria*	1	4	fr.	1	4	May be N-fixing
H.	*Aster ericoides*	1	4	fl.	1	4	
H.	*Bartonia virginica*		4	fr.	1	4	Mycorrhiza
T.	*Polygala nuttallii*		4	fl.	1	4	
Ch.	*Polytrichum commune*	1	4	fol.	1	1	contributes acidity
E.	*Cladonia* sp.	2	3	fol.	4	23	
	Outside of quadrat						
P.	*Vaccinium vacillans*		3	fol.	1	4	
H.	*Lespedeza capitata*		4	fr.	1	4	
H.	*Juncus greenei*		4	fr.	1	4	

P.	*Betula populifolia*		1	fol.	1	4	Dwarf, feeble
P.	*Prunus serotina*		1	fol.	1	4	Dwarf, feeble
H.	*Rubus villosus*		2	fol.	1	4	
H.	*Lespedeza virginica*		4	fr.	2	4	
H.	*Eupatorium hyssopifolium*		4	fl.	1	4	
G.	*Aletris farinosa*		4	fr.	1	4	
H.	*Viola fimbriatula?*			fol.			
H.	*Cirsium discolor?*		4	fol.			
G.	*Apocynum androsaemifolium*			fol.			
T.	*Linum medium*		4	fl.			
H.	*Desmodium marylandicum*		4				
H.	*Solidago nemoralis*		4				
T.	*Gerardia setacea*		4				
P.	*Gaylussacia baccata*		4				
P.	*Quercus marilandica*		4				
P.	*Salix tristis*		4				
H.	*Solidago odora*		4	fl.			

Dicranella heteromalla in dense sods several dm. across was found under grass in the shade of *Quercus marilandica*. *Polytrichum commune* is common and widespread, and *P. piliferum* is sparsely distributed in dry sunny places where 10-20cm. of sand is exposed between the clumps of grass. *Ditrichum tortile* is on smaller, shaded bits of ground.

A comparison of the species lists and social relations of *Andropogonetum scoparii* of High Hill, and others described under Assoc. 45 with *A. Hempsteadi* reveals many resemblances. The first, however, is very poor in species, the second very rich. The first is a very characteristic stage in the revegetation of abandoned agricultural land. It is stable for long periods of years, and follows, often rather quickly, the ruderal communities. The second is a very old, stable, natural community, prehistoric. Like the western prairie, when disturbed it restores itself very slowly, if at all. We find then, the older community richer in species than the newer, contrary to usual expectation.

Andropogonetum Hempsteadi is even more nearly related to Pine Barren, as the species lists plainly show. In fact, at "Island of Pines," south of Hicksville on Highway 24, a grove of *Pinus rigida* bounds the Plains on the southeast. The ecologic difference between conditions for *Pinetum rigidae* and *Andropogonetum Hempsteadi* are very slight. The Plains have a more porous substratum of pure quartz pebbles. A dense growth of grass adds vastly more humus to the soil than a growth of trees. In Iowa, wholly different soils are built on the same mineral substratum when trees or grasses occupy the terrain. Sloping terrain favors trees, giving a pale grey soil, clayey and poor in humus. Level land favors grasses, whose residues give a rich black humus that crumbles exquisitely under cultivation. A similar humus, more peaty because of high rainfall, covers the Hempstead Plains. The Soil survey classifies most of the Plains as Hempstead Loam, but in places this vegetation

is on Sassafras loam, Sassafras sand, Mineola gravelly sandy loam and Dukes loamy sand.

All of the *Andropogoneta* of Long Island clearly belong to the same Alliance or *Andropogonion*. Those of the tall grass prairie must be placed in another Alliance, but all together are members of the order *Andropogonetalia*.

5. Zone Associations of Streams and Ponds

As there are all gradations from open water of springs, streams and ponds to wet ground and dry, so there are all gradations in the aggregation of species. Nevertheless, distinct and characteristic communities occupy the water and margins of water. From the composition of these communities it is possible to predict the kind of substratum upon which they grow, and the type of dry-land vegetation to which they belong even though the procedures of agriculture sometimes tangle the threads of social relationship. Since these associations often occur in adjacent strips, related to the amount of soil water, they may be called zone associations. It seems helpful to consider them in relation to the adjacent major vegetation as those of (1) the Deciduous Forest, and those of (2) the Pine Barrens. But these categories are by no means sociologically distinct.

A.—Of the Deciduous Forest Area

a.—Springs, streams and fresh marshes

Moss associations

The cold springs which give the name to the Harbor are mostly broad stretches of cold seepage, 10 to 100m. wide, along the bases of the hills, shaded immediately by birch and beech, and at greater distance by oak and chestnut. On the seeping sand and gravel liverworts and mosses abound: *Lophocolea bidentata* on small stones, *Brachythecium rivulare* and *Bryhnia novae-angliae* on sticks, *Eurhynchium rusciforme* on fine gravel near the lake margin; *Riccia fluitans* close to the First lake; *Mnium punctatum elatum* in deep shade at head of First lake. The borders of these seeps are sodded with *Mnium hornum, Dicranum flagellare, Georgia pellucida, Leucobryum glaucum, Pallavicinia lyellii, Odontoschisma prostratum, Hypnum imponens*. The evidence indicates that these are members of *Betuletum*, here in fragmentary form. Seeps with abundant humus harbor *Chrysosplenium americanum* (Assoc. 47).

When the seepage is gathered into a small stream, beds of water cress *(Radicula nasturtium-aquaticum)* compete with *Callitriche palustris*, (Assoc. 48). Similar streams are conveyed through concrete channels at the N. Y. State Fish Hatchery. Here the walls are covered with *Amblystegium irriguum* at the splashing intake, with *A. riparium fluitans* and *Chiloscyphus rivularis* near by. In quieter places *Brachythecium rivulare* extends from 10 or 20cm. above water to 2cm. below; *Climacium Kindbergii* grows just beneath the water surface, and *Fontinalis novae-angliae* var. *Grouti* Welch flourishes at 2 to 30cm. depth. The walls above water carry dense wide luxuriant sods of

Marchantia polymorpha, with abundant gemma cups and "umbrellas" of both sexes, but without sporophytes. In one stream *Fontinalis lescurii* was found; in two others *F. gigantea;* in another the decidedly southern *Sciaromium lescurii.*

The margins of fresh running streams may be shaded by *Alnus rugosa* (often beset by *Exoascus alnitorquus*), *Salix sericea* or *Benzoin aestivale,* and by forest trees of the adjacent woods. On cleared land the stream may be accompanied only by a dense, tall (1m.) ribbon of *Impatiens biflora,* with an occasional *Cyperus strigosus.* A wider band of the wet ground acquires more and more species leading to one or other of the following associations, 49 or 50.

49. *Tall Herb Association of a Wet, Neglected Meadow*

Above the Drum factory is a tract of several acres occupied by a tall (1-2m.) growth of mixed herbs which we have not attempted to study quantitatively. The wetter portions are occupied by *Typha latifolia.*

The remaining portion is a riot of *Impatiens biflora, Mimulus ringens, Scirpus cyperinus, Glyceria canadensis, Leersia oryzoides, Aspidium thelypteris, Polygonum arifolium, Onoclea sensibilis, Vernonia noveboracensis* and *Eupatorium purpureum.* Beneath *Scirpus, Polygonum* and *Glyceria, Sphagnum* sp. is found.

This association requires constantly flowing fresh water. The soil may be water logged, but not stagnant. Doubtless the O-content of the substratum is relatively high.

A similar association is gradually filling up a small pond on Highway 25A, fed by cold spring water. Next to the open water is a 1m. zone of *Callitriche palustris;* then ½-1m. of *Veronica anagallis-aquatica,* then 1m. of *Bidens comosa.* An area of 30m. across is full of *Impatiens biflora,* with beds ½m. across of *Polygonum sagittatum* on the wetter margins. Two stalks of *Typha latifolia* (ster.), a few of *Scirpus cyperinus,* and several of *Cicuta maculata* (H) are sacttered about the association on the deep muck substratum. The adjacent land is occupied by *Salix sericea,* clambered over by *Amphicarpa monoica* and *Humulus lupulus.* A marginal spot 2m. across has the characteristics of open marsh: *Carex lurida, Juncus effusus, Cyperus strigosus, Aster puniceus, Equisetum arvense, Eupatorium perfoliatum.* This is a fragment of the next association.

50. *Carex lurida Association*

Open marshy meadows occur, where constantly seeping fresh spring water keeps the substratum sweet. Something of this kind is oft-repeated, but we have not attempted to study it quantitatively. The average height of the plants is almost 1m. A small stand near the Sandspit on the hither side of the boundary of the "Borough of Laurelton," yielded the following list of plants. Conspicuous in the total cover:

Carex lurida
Polygonum arifolium
Juncus accuminatus
Onoclea sensiblilis (soc. 5)
Mentha piperita
Juncus effusus
Impatiens biflora
Leersia oryzoides

Of small cover value:

Lobelia cardinalis
Symplocarpus foetidus
Saggitaria latifolia.
Hypericum mutilum
Cyperus ferax

The marginal zone is filled mostly with *Solidago rugosa.* The proportions of the different members of this community differ materially from wet seasons to dry, and according to whether the area is closely mowed or allowed to grow naturally. The field of which this is a corner is regularly mowed for hay, and frequently pastured by cattle after mowing. Some such *Carex-Juncus* association is to be expected under like conditions in the Oak-Chestnut area of southeastern Pennsylvania.

51. *Thelypteretum*

Aspidium thelypteris	5:4	*Scirpus americanus*	+:4
Erechtites hieracifolius	+:4	*Hypericum canadense*	+:4
Aster novae-belgii	+:4	*Hypericum mutilum*	+:4
Impatiens biflora	+:4	*Hypericum virginicum*	+:4
Asclepias incarnata	+:4	*Eupatorium perfoliatum*	+:4
Myrica caroliniana	+:2	*Panicum* sp.	+:1

A dense growth of ferns, 2 ft. tall, covers a portion of the Cold Spring Harbor saltmarsh. *Scirpus americanus* overtops the fern, its stalks being 1 to 3 ft. apart. The other species noted are insignificant in volume. The margins of the fern bed are abrupt; there is no straggling out of ferns into adjacent vegetation. But the ground level is exactly even with that of the rest of the saltmarsh.

The soil in this *Thelypteretum,* however, is not salty, even though it is submerged about a foot at extreme high storm tides. Immediately after the fall of such a tide, samples of water were taken by scraping little depressions and allowing them to fill by seepage. Tests made by Dr. Martha Washburn of the Laboratory Staff showed:

From inner margin of *Thelypteretum* adjacent to *Typhetum* ---------- 0.044% NaCl
From middle of *Thelypteretum* ---------- 0.068% NaCl

This bears out the conclusion of Conard & Galligar (1929) that seepage of fresh water from the land maintains the associations on the margin of the saltmarsh.

Thelypteretum, in form similar to this, is often met in New England, eastern Pennsylvania, and rarely in eastern Nebraska. *Asclepias incarnata, Eupatorium perfoliatum, Impatiens biflora, Hypericum canadense* and *H. mutilum* are to be expected as associates. The site is always marshy and poorly drained. Wiegand and Eames assign the fern to "Boggy meadows, pond shores, and ditches, in acid or slightly calcareous soils * * * Newf. to Man., southw. to Fla., La., and Tex. *** Eurasia."

b. Undrained Ponds

The first thing that strikes the eye is the very great difference in the plant populations of the many ponds in this area. They have not been examined for oxygen content of the water and soil, nor for dissolved nutritive salts. Miss Ruth Patrick made a report (unpublished) on pH of the waters of four of these ponds with findings as follows:

	Water	*Adjacent soil*
Polygonum Pond	7–7.3	6.8–6.5–6.2 Salix sericea
Decodon Pond	6.4–6.9	6–6.3
Moss Bog, High Hill	5.6–(mold)	6.0 ft. (at 12 in. deep)
Clear Pond, High Hill	5.6–6.0	6.5–6.4

Acretum 5.9 near surface 6.0: for *Acer* roots (near Decodon Pond).

Miss Patrick used both colorimetric and electrometric methods, and made determinations both in the field and in the Laboratory. From appearances we have also to do with eutrophic, oligotrophic and dystrophic waters (Thienemann, 1926). Unquestionably there are *fresh* ponds with flowing, oxygenated water, and *stagnant* ponds with many stages and proportions of decaying organic matter, where the oxygen content must be very low. Under these two headings one can only describe the ponds individually, one by one.

52. *Euglena Ponds*

Two shallow glacial "kettles" occur on the hills near the laboratory, in cultivated grounds, near barns. These are completely covered in summer with *Euglena* spp. Large areas are green (active stage). Other large areas are red (encysted). Light winds mix these growth stages in long interlacing streamers. The earth on the margin of such a pond dries as the water recedes, and cracks in polygonal chunks. Damp surfaces are often overgrown with *Vaucheria* sp. The walls of the crevices may be crowded with *Botrydium* sp. Other vegetation is scarce or lacking in and immediately around such ponds. On permanent shores *Gratiola aurea* is sometimes abundant and *Eleocharis obtusa, E. acicularis, Myriophyllum humile, Ludwigia palustris, Ilysanthes dubia,* and *Eclipta alba* may be found.

53. *Extinct Pond north of Woodbury Bog*

This small kettle held perhaps 3dm. of water at its deepest stage, much of this drying away in summer. In 1927 there was a zone of bare muck around the water, then a well mixed zone of *Eleocharis acicualris, Myriophyllum humile* and *Gratiola aurea.* Outside of this was a zone of *Ludwigia palustris, Callitriche deflexa Austinii, Proserpinaca palustris, Eleocharis obtusa, Juncus acuminatus, Alisma plantago-aquatica, Hypericum virginicum, H. mutilum, Ilysanthes dubia,* and *Sphagnum* sp. Two more zones merge into ordinary terrestrial vegetation: first, *Aspidium Thelypteris, Ambrosia artemisiifolia, Hypericum virginicum, H. mutilum, Galium claytoni, Lycopus* sp.; second, *Rubus villosus, Onoclea sensibilis, Steironema lanceolatum, Asclepias incarnata pulchra, Aspidium thelypteris, Carex* sp., *Lycopus* sp. The little pond was then surrounded by cultivated ground. Now (1934) it is part of a lawn, excavated, walled, and planted with hybrid waterlilies. In 1910 the water sup-

ported a tiny *Potamogeton*, probably *P. dimorphus*. *Rhexia virginica* and *Lysimachia terrestris* have been reported from the middle zone.

54. *The Clear Pond on High Hill (Patrick)*

"Near stake 324 on High Hill" Miss Patrick examined a pond with "very clear" water, containing *Ulothrix, Oedogonium,* desmids and diatoms. "The pH of the water varies from 5.6 to 6.0." The pond was completely surrounded and hidden from view by *Acer rubrum,* growing in a soil with pH 6.2-6.4. The very scanty vegetation around the pond consisted of *Catharinea crispa, Dicranella heteromalla, Hypnum haldanianum* (on a log), *Leucobryum glaucum, Pohlia nutans, Pallavincinia lyellii.*

55. *Moss Pond on High Hill*

On the northeast slope of High Hill is a small kettle which sometimes has open water, and at other times only wet muck. In 1933 and '34 one could walk across it dry shod. Miss Patrick examined it when there was no open water, but a complete carpet of *Drepanocladus fluitans*. In wet seasons this moss is the var. *gracilis*, but in dry seasons it becomes var. *Jeanbernati*. The muck had a pH of 5.6 near the surface, and 6.0 at a depth of 3dm. The pond is completely shaded by tall trees of several kinds.

Fig. 17. *Polygonum amphibium* pond, Woodbury, 1928. The author in the background collecting *Anthoceros* and *Riccia*.

56. *Polygonum Pond*
(Fig. 17)

Northeast of Woodbury Bog, north of Highway 25, is a pond covering about an acre, in another shallow kettle, surrounded by cultivated ground. It is subject to great changes of level, but the water is never over 6dm. deep, usually half that. In August, 1933, there was no water visible. Miss Patrick

found the pH of the water 7 to 7.3. Freshly exposed earth around the margin gave a pH of 6.8; this soil was covered with unicellular green algae, with *Botrydium* in the crevices. Around this is a zone 6-8m. wide of *Polygonum amphibium,* erect or floating according to circumstances. The soil for this measured pH 6.5. A zone surrounding this has *Alisma plantago-aquatica, Ludwigia palustris, Steironema ciliatum, Galium claytoni, Penthorum sedoides, Hypericum virginicum, Aster ericoides, Scirpus sylvaticus, Carex lupulina, Eupatorium purpureum, E. perfoliatum.* And on the earth between these, *Anthoceros laevis, Riccia sullivantii* and *R. Beyrichiana. Myriophyllum humile* and forma *natans* have been found in this pond. And *Gratiola aurea* is usually abundant from shallow water to firm ground. A shrubby border includes *Salix sericea* and *Cephalanthus occidentalis.*

57. *Decodon Pond*

(Fig. 18)

A small pond at the south end of Woodbury Bog was found by Miss Patrick to have a pH of 6.4-6.9. About ¾ of the margin of the pond carries

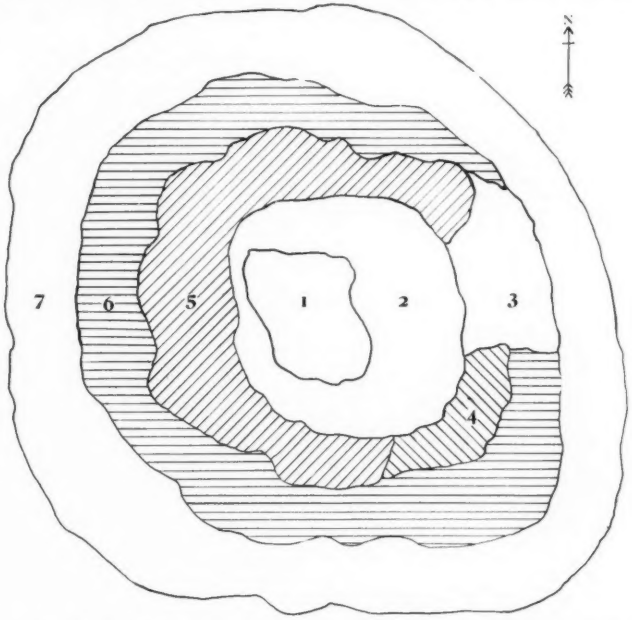

Fig. 18. Diagram of *Decodon Pond* at Woodbury Bog. By Ruth Patrick. 1, open water, pH 6.4-6.9; 2, bare mud; 3, miscellaneous plants near highway; 4, *Cyperus* sp., pH 6.3; 5,*Decodon verticillatus,* pH 6.0; 6, *Rubus allegheniensis,* pH 6.1; 7, *Acer rubrum,* pH 6.0 at surface, 6.2 among roots.

a dense exclusive growth of *Decodon verticillatus,* in a soil with pH 6. Back of this is a zone of *Rubus allegheniensis* in a soil with a pH 6.1. The edge of the pond not occupied by *Decodon* is covered with *Cyperus ferax? (C. erythrorhizus,* 1934) with a soil of pH 6.3. *Aceretum rubri* completely surrounds the pond, with a surface pH of 6.0 (in *Sphagnum* peat), and a deeper layer of 6.2 where the tree roots are.

This pond and *Aceretum* are transitional between the oxylophyte vegetations of the Deciduous Forest Region and the Pine Barrens.

c. *Drained Ponds*

Our only ponds with constantly flowing water are artificial. A small pond on Highway 25A has already been mentioned under Association 49. The open water of this pond always has a rich green bottom-mat of *Spirogyra.* One year it was teeming with *Volvox aureus* about August 1.

Three large ponds, 5 to 20 acres each, have stood for over a hundred years in the valley south of the Harbor. The farthest south, known as III Lake, is doubtless fed primarily by three small streams which flow toward it but disappear ¼ to ½ mile from it . In addition, all of the ponds are fed by springs along the base of the hills. Only along the lowest pond, I Lake, are these springs conspicuous and above water level. Their moss communities have already been described. Obviously, III Lake has the least flow of water through it, and I Lake the most. The water is clearest in I Lake, most stagnant in III. The vegetation at the head of III Lake is strongly suggestive of an acid dystrophic substratum. That at the head of I Lake lacks this character. The margin of III Lake has large beds all along the west side of *Drepanocladus exannulatus,* 10-15cm. long, stretching 2-3cm. above the water with its hooked tips. On shore *Aulacomnium palustre* and *Sphagnum* spp. share the area, the latter greatly predominating. Shallow wet margins or half-submerged logs in all of the lakes carry *Gratiola aurea,* and *Hypericum virginicum.* The marginal *Sphagnum* of III Lake accommodates *Drosera rotundifolia.* The shallows of I Lake include a bed of *Calliergon cordifolium,* which in turn is a home for myriads of desmids.

The center of I Lake has 3 beds (clones) of *Nymphaea odorata Ait.; Brasenia peltata* has been found in this lake also. The margins of II and III Lakes have beds several meters in extent of *Sparganium* sp. with *Coleochaete* sp.; other beds of *Typha latifolia;* patches of *Potamogeton* sp.; *Nitella* sp. The head of II Lake is a very wet grassy, stagnant marsh, which I have never carefully examined.

One might certainly speak of:

58. *Gratiola aurea—Hypericum virginicum* ass'n.
59. *Potametum.*
60. *Typhetum.*
61. *Sparganietum.*

Other associations will be recognized when the ponds are more minutely studied.

62. *Fruticetum at Head of III Lake*

The transition from water to land at the head of III Lake is through a bog of shrub-covered islands. This area was studied by Miss Vera Kenney (Mrs. E. T. Boardman) in 1927, from whose paper (unpublished) the following description is largely drawn.

The adjacent woodland is *Aceretum rubri*. The outermost emerged vegetation is *Caricetum strictae*.

The shrub islands "seem to have been originally *Carex stricta* tussocks on which seedlings of more terrestrial plants" have taken hold. "The interesting thing was the diversity of species a single 'two by four' island could maintain. For instance, investigation of one tussock, covering not more than 9 square yards if that, yielded this list:

1 *Acer rubrum*—tuft of leaves at top of 7-8 ft. sapling.
1 *Pyrus arbutifolia*—4-6 ft.
2 *Clethra alnifolia* 2½-3 ft.
1 *Rosa carolina* 2 ft.
2 *Vaccinium corymbosum* 2 ft.
Cuscuta sp.
Acer rubrum sdl.
Ilex verticillata
2 *Rhododendron viscosum* 3-5½ ft.
1 *Alnus rugosa* 2½ ft.
1 *Viburnum dentatum* 1 ft.
Hypericum virginicum
Drosera rotundifolia
Carex sp.

Another clump had:

Clethra alnifolia
Lyonia ligustrina
Carex stricta, one tussock.
Rhus vernix
Rhododendron viscosum

Another had:

Sambucus canadensis
Alnus rugosa
Clethra alnifolia
Rhododendron viscosum.

Such clumps are usually covered and margined densely with *Sphagnum* sp. If any peaty surface exists, it is covered with *Odontoschisma prostratum* and *Cephalozia* spp. Where the clumps, farther landward become continuous, we have the transition to *Aceretum*.

63. *Caricetum strictae*

Of this association Miss Kenney gave a record of one-meter quadrat, having:

Carex stricta tussocks
Impatiens biflora (1 or 2)
Juncus effusus
Polygonum sagittatum
Bidens sp.
Leersia oryzoides.
Rosa carolina
Eleocharis intermedia
Viola sp.
Polygonum arifolium
Polygonum persicaria?
Epilobium adenocaulon

The plants other than *Carex stricta* are "much in a minority from the cover standpoint." Elsewhere among *C. stricta* Miss Kenney records:

Eupatorium purpureum
Sphagnum sp.
Scirpus sylvaticus
Arisaema triphyllum
Sparganium sp.
Symplocarpus foetidus
Osmunda cinnamomea
Onoclea sensibilis
Aspidium cristatum

This is either a compilation from several places, or a distinctly transitional stand.

B.—Of the Pine Barrens

Associations 40-44 above are woody plant associations of wet ground. Association 28 also is essentially a Pine Barren association. There remain certain marsh and pond associations to be described. These are epitomized in the zones surrounding a small pond north of Lake Ronkonkoma. This lake was without visible water in August, 1933, but the central portion was too soft to walk upon. Where the water is 3-5dm. deep, as is usually the case, it is dotted with large colonies of *Nuphar advena*, smaller colonies of *Nymphaea odorata*, a few plants of *Brasenia schreberi*, and a general scattering of *Nymphoides lacunosum* (Assoc. 64). All of these were present on the muddy surface in 1933. In water 1-8cm. deep is usually a zone of *Eriocaulon septangulare, Gratiola aurea, Eleocharis acicularis, Myriophyllum humile* (Assoc. 65). In 1933 *Eriocaulon* covered the entire lake bed making a soft white meadow! The next firmer zone consists of *Rhynchospora glomerata, P. alba, Xyris caroliniana, Cyperus dentatus, Juncus dichotomus, J. pelocarpus, Hypericum mutilum, H. canadense, Drosera longifolia*, and *D. rotundifolia* (Assoc. 66). Above this is a conspicuous zone of *Agrostis hyemalis, Leersia oryzoides*, the above Junci, *Rhexia virginica* (Assoc. 67). Upon this follows a shrub zone of *Vaccinium corymbosum, Rhododendron viscosum, Alnus rugosa, Clethra alnifolia, Pyrus arbutifolia*, and *Acer rubrum*, all 2-3m. tall (Assoc. 42). This entire lake and shore series is about 30m. x 40m.—an even broad, oval area.

Changes in water level seriously displace the neat zonation described above, as we have already indicated. Graham and Henry (1933) have studied this shifting of zones in some glacial kettles near Wading River. They found in a certain pond a central area of aquatics: *Callitriche heterophylla, Potamogeton Robbinsii, P. hybridus*. Around this was a shore-zone of *Eriocaulon articulatum, Juncus articulatus, J. dichotomus, J. pelocarpus*. The next zone consisted of *Coreopsis rosea, Cyperus* sp., *Gratiola aurea, Juncus articulatus, Polygonum hydropiper*. Zones 4, 5, and 6 are distinctly terrestrial.

As the lake recedes certain hydrophytes are left stranded above water. The more tolerant of these may remain for a time in the first shore zone and are sometimes found there with some of the more mesophytic forms. Similarly during periods of rising water level, particularly when the rise is rapid, certain submerged mesophytes may survive for a short time with the invading hydrophytes. (p. 302-303).

A pond nearer to Lake Ronkonkoma, and the marsh at the north edge of the Lake, have *Decodon verticillatus* marching out into the water. The stems of this shrub arch over and touch the water ½-1m. from the point of origin. At once roots are sent out, a thick corky aerenchyma develops around the rooting stem as in *Jussiaea*, new shoots start upward, also surrounded by corky aerenchyma, and a new outpost of *Decodon* is established. Between these outposts *Sphagnum* gradually fills in, often forming a floating bog. In this,

Chamaedaphne calyculata becomes established. *Decodon* dies out and the *Chamaedaphne* association arises (Assoc. 43). Cf. Assoc. 57. On the resulting deep peaty substratum *Vaccinietum corymbosi* (42) normally follows.

The marsh on the north edge of Lake Ronkonkoma has yielded also *Sarracenia purpurea, Utricularia purpurea, U. vulgaris, U. minor, Eriophorum virginicum, Calamagrostis canadensis, Dulichium arundinaceum, Pontederia cordata, Lachnanthes tinctoria, Lycopodium inundatum,* and *L. carolinense.* The social relations of these interesting plants have not been determined. The station is nearly destroyed by real estate "improvements." On the trampled beach of Lake Ronkonkoma, *Cyperus dentatus* and *Juncus* sp. form almost a distinct zone, mingled with *Juncus greenei,* a character plant of the Hempstead Plains (46)!

68. *Low Shrub*

Another type of marshy ground supports a mixture of *Aster umbellatus, Sphagnum, Lilium philadelphicum, Osmunda cinnamonea, Woodwardia virginica, Gaultheria procumbeus, Habenaria blephariglottis, Ilex glabra, Gaylussacia dumosa, Vaccinium corymbosum, Pyrus arbutifolia,* and *Polygala lutea.* This combination is seen on Santapogue River, northwest of Babylon, between Highway 109 and the railroad. It is repeated in the Pine Barrens in New Jersey.

The zonal arrangement on the west bank of Santapogue River has *Quercetum ilicifoliae* (39) on upland, then the above low shrub association, then a tall shrub association (42), and along the stream *Aceretum osmundaceum* (40).

The following list gives a comparison of these associations:

Santapogue River near Babylon, between Highway 109 and railroad south of highway. August 20, 1934.

Species list with covergrade	Upland woods	Aceretum	Tallshrub swamp	Low shrub	Sphagnetum
Pinus rigida	+				
Quercus ilicifolia	5				
Quercus prinoides	+				
Chrysopsis mariana	+				
Chrysopsis falcata	+				
Vaccinium pennsylvanicum	3				
Gerardia pedicularia	+				
Desmodium rotundifolium	+				
Eupatorium hyssopifolium	+				
Pteridium aquilinum	+			+	
Lespedeza capitata	+				
Lespedeza hirta	+				
Lespedeza sp.	+				
Arctostaphylos uva-ursi	+				
Andropogon scoparius	+				
Asclepias amplexicaulis	+				
Baptisia tinctoria	+				

Species list with covergrade	Upland woods	Aceretum	Tallshrub swamp	Low shrub	Sphagnetum
Sericocarpus asteroides	+				
Sericocarpus linifolius	+				
Betula populifolia	+		+	+	
Acer rubrum		4	1	+	
Gaylussacia dumosa				3	
Gaylussacia frondosa			+		
Drosera rotundifolia			+	+	+
Eriophorium virginicum					+
Sphagnum cymbifolium?			+	+	5
Sphagnum acutifolium?		1	3	3	2
Sphagnum sp.				+	
Eupatorium teucrifolium				+	
Rhynchospora alba					+
Carex sp.		+			
Hypericum virginicum					+
Osmunda cinnamomea		+	+	1	
Osmunda regalis		+			
Eupatorium purpureum				+	
Calamagrostis cinnoides			+		+

6. Culture Associations

If man is a natural object, and a product of nature, his influences upon vegetation must come within the scope of the naturalist. These influences are so far-reaching and unique that they demand a separate treatment. The resulting associations we are calling "Culture Associations."

If human intervention is constant and orderly, a fixed and definite association is maintained. If the intervention is irregular and fluctuating, the vegetation fluctuates, just as it does with long time fluctuations of weather. (cf. Henry; Clements, 1934). Regular procedures give us gardens, lawns, pastures, mowing fields, plow-land, managed forests. If any of these is neglected for a year, characteristic changes in the vegetation take place, continuing through more or less definite stages for many years. Eventually an end stage or "climax type" of vegetation, more or less permanent and self-sustaining, results which will resemble the original vegetation of the area, but it is not likely to be identical with it. If at any point during the period of neglect human intervention again comes in, one of the distinctive anthropogenic associations is restored. The season of the year at which human intervention begins, or ceases, greatly affects the first resulting types of vegetation.

We must consider then:

1. Cultivated Gardens, 69.
2. Abandoned Gardens, year by year.
3. Lawns, 70.
4. Abandoned Lawns, year by year.
5. Mowing fields, 71.
6. Abandoned mowing fields, year by year.
7. Pastures, 72. Not studied.
8. Abandoned pastures, year by year.

9. Plow-land, 73. Not studied.
10. Abandoned plow-land, year by year.
11. Cut-over woodland (slash), 74. Not studied.
12. Abandoned slash, year by year.
13. Paths and wagon-tracks in forest and grassland, 75. cf. Clements, 1934. Not studied.

The sequence of associations, and their composition is more or less different in the areas of the three major vegetation types: deciduous forest, pine barren, Hempstead Plain. The study of Culture associations by sociological methods has scarcely been started in this vicinity. The most important work of the kind in America is that on range management in the West. Just as large a field of investigation is at hand in the East. Agriculturists can tell a good deal about a soil and its needs by inspecting the vegetation upon it. Careful quantitative studies should yield very reliable indications to guide the cultivator.

69. *Cultivated Gardens: Portulacetum*

Every flower or vegetable garden in the deciduous forest area of this vicinity, no matter how faithfully tended, has as unbidden guests: *Portulaca oleracea, Galinsoga parviflora, Mollugo verticillata* (usually).

Portulaca can bear but little shade. A factor in this intolerance is the increased incidence of *Albugo portulacae*. The weed often occupies denuded areas in proximity to cultivated ground to the exclusion of everything else. It was so in 1928 on the margin of a road which was cut through a mowing-field during the previous winter. The next year not one *Portulaca* was found there; the place was overgrown with tall weeds: *Ambrosia artemisiifolia*, etc. The same relation exists in s.e. Pennsylvania. *Portulaca* is similarly prevalent in central Iowa, but Galinsoga is still strictly local in that state.

Abandoned gardens are occupied the first year with tall weeds, e.g. *Amaranthus retroflexus*. *Galinsoga* and *Mollugo* survive for a time in the shade of these. The place of *Chenopodium album, Erigeron canadense, Ambrosia artemisiifolia* and species of *Solidago* has not been worked out, but they all have a part in the procedure.

The course of events in the regions of Pine Barrens and Hempstead Plains has not been studied.

70. *Lawns*

The best kept lawns are not pure stands of *Poa annua* or *P. pratensis*. Both are used, but the latter predominates. *Agrostis alba* forms are usually present. And in late summer and autumn most lawns are surfaced principally with *Digitaria sanguinalis*. The rosettes of *Hypochaeris radicata* abound about the Laboratory. In damp, closely clipped lawns *Selaginella apus* makes yellowish spots, and one lawn has an almost complete cover of *Hydrocotyle*. This was seen also on the White House lawn in Washington, D. C. Mushrooms *(Agaricus campestris)* are common in August and September.

The Laboratory lawns are only cut occasionally, and with a scythe. Much

of the area is covered with *Dactylis glomerata*. Amongst the grass roots, and along the sides of buildings several mosses are found. The commonest, perhaps, among the grass roots, is *Eurhynchium hians*. Near Blackford Hall *Mnium cuspidatum* covers the ground in shade, with *Brachythecium salebrosum* or *(B. oxycladon)* in partial shade. Just such an arrangement occurs on the north sides of buildings on the campus of Grinnell College in Iowa. The mosses of the Campus at Cold Spring Harbor were studied in detail by Marian Parker (1932). The abandoned lawn has not been studied.

71. *Mowing Fields*

An old field at the west side of the Laboratory property has been mowed annually for many years, but for the rest has been left entirely to itself. The valuable grasses here are *Dactylis glomerata, Agrostis alba, Anthoxanthum odoratum,* and *Poa pratensis;* of less value are *Andropogon scoparius, Tridens flavus, Poa compressa.* This field is apparently on the way to become an *Andropogonetum.* A number of meter-quadrat studies are summarized below. For each species covergrade (CE) and vitality is given.

Summary of 7 one-meter quadrats recorded in 1933 and 1934.
Neglected Hay Land

Andropogon scoparius	4:4	*Plantago lanceolata*	2:4
Aster ericoides	+:4	*Eragrostis pectinacea*	+:3
Solidago juncea	+:	*Cladonia* sp.	+:3
Catharinea angustata	1:3	*Polytrichum commune*	+:3
Cirriphyllum Boscii	+:3	*Panicum sphaerocarpon*	+:4
Coleosporium solidaginis	+:4	*Ambrosia artemisiifolia*	+:3
Daucus carota	+:2	*Asclepias syriaca*	+:1
Tridens flavus	+:4	*Rhus toxicodendron*	+:2
Rumex acetosella	+:2	*Solidago memoralis*	+:2
Anthoxanthum odoratum	+:3	*Cyperus filiculmis*	+:4
Agrostis alba	1:3	*Poa pratensis*	1:3
Hypochaeris radicata	+:1	*Chrysanthemum leucanthemum*	+:2
Fragaria virginiana	+:4	*Juniperus virginiana*	+:3
Oxalis stricta	+:3	*Rubus villosus*	+:2

The neighboring field was wholly abandoned a few years ago. Its lesser vegetation is similar to that of the mowed field. In addition, clumps of *Myrica carolinensis* are increasing, *Juniperus virginiana* has many representatives up to 1.5m. tall, *Betula populifolia* 1m., and there is an abundance of *Solidago rugosa* and *S. canadensis,* flowering freely.

Apparently the usual fate of all kinds of agricultural land is to give place to *Andropogonetum.* In this *Juniperus virginiana* takes hold, along with *Myrica carolinensis,* and any adjacent trees and shrubs. Ultimately the type of woodland appropriate to the soil-type is restored (cf. Blizzard, 1931).

Part III.—Succession

In a succinct and exquisitely expressed paper on "The Relict Method in Dynamic Ecology" Clements (1934) has presented the ripe fruit of his abundant study of plant succession. From this admirable paper one hesitates to

pick out even a single sentence with which to disagree. It is obviously true that (p. 41) "Though a knowledge of 'what is on the ground' is both indispensable and prerequisite, by itself it represents but a segment of the dynamic flow of processes." But it does not necessarily follow that "Taken alone its facts are deficient in meaning or actually misleading, and it is solely by placing them in the proper setting as to time and events that they gain their true significance," except for the sole purpose of studying succession.

On the contrary, it is to be regretted that American ecology has been so completely dominated by the dynamic idea. We have pursued embryology and phylogeny and geographical distribution of vegetation to the almost complete neglect of the anatomy and physiology and taxonomy of the associations under consideration. Attempting to follow the lead of our acknowledged masters Clements and Cowles, many of us have made premature attempts to force a seral arrangement upon the communities which we study, and have fallen into grievous errors.

The Successional Relations of the Associations

In a paper published in 1913, Transeau presents a view of the littoral succesions in the Vegetation of Cold Spring Harbor. His figure 8, a diagram of the "successions," is rather a chart of the zones. It is difficult, for example, to see how the "Eel grass formation" on "mud and sand" can lead up, as the arrow indicates, to the "Rockwood Formation" *(Fucus* and *Ascophyllum)* on boulders and stone walls. It is equally difficult to imagine the "Rockweed Formation" leading up to the "*Spartina cynosuroides* Association" on fine silty mud—the more so, since rocks are naturally exposed only on points where erosion is violent and *Spartinetum glabrae* occurs only where fine silt is being deposited. Nor is there any place where the *Prunus maritima* association merges into Pine Barren. It would hardly be fair to criticize a paper twenty years old, if it were not for the fact that Zonation is still taken as an index of succession. Graham and Henry (1933) refer to zones as equivalent to stages in a sere. But there is no way for upland Pine Barren vegetation to invade a bed of peat without first getting rid of the peat. And no way of doing this is proposed for the bottom of a kettle hole. To speak of pine wood's as an end stage in a "hydrosere" is hypothetical, if not actually misleading. Clements in 1916 stated and in 1928 reaffirmed "Zonation is the epitome of succession. In short, zones are stages." This view leads to such large and obvious errors as are pointed out above. And Gleason has already noted (1927) that "Areal zonation of vegetation does not constitute a sere, and is correlated with succession only in exceptional cases."

Zones often occur on account of the presence side by side of profoundly different substrata. The only way in which vegetation can produce a uniform soil on all kinds of mineral substrata is by accumulation of enough peat to eliminate the influence of the substratum. But so-called climax associations are not often found on peaty soils. And applying the long-time view of Cowles, it is hard to see how any number of erosion cycles can produce identical soils out of Archaean crystalline rocks on the one hand and Palaeozoic limestones on the other.

Miss Henderson (1933) after a very interesting descriptive paper, felt obliged to discuss "Plant Succession" in the area studied. But she remarks very judiciously that "the stages of succession are rather difficult to work out." p. 7.

The elaborate terminology invented by Clements for the naming of seres, and stages in the sere, is useful in those cases where seral relations are not wholly hypothetical. And it is well in all cases to try to discover whence our associations have come and whither they go. But any attempt to force all of the associations which we find into a seral scheme is sure to lead to disaster, as was pointed out above. Many associations, like many species, may be known structurally long before their ontogeny or phylogeny is known. And doubtless many seres, like many plant and animal phyla, end in a *cul-de-sac*, without reaching the "climatic climax".

A long-time study of succession at Cold Spring Harbor was initiated by Johnson & York (1914). Later reports by Conard (1923) and Conard and Galligar (1929) have shown how very slow is vegetational change under natural conditions. Conard (1911, 1923) has studied the revegetation of a denuded area, obtaining some data on the development of soil, and the establishment of *Andropogonetum* and *Quercetum*. Blizzard (1931) showed the composition of *Andropogonetum scoparii* from pasture land, and the invasion of shrubs and trees into it. Kenney (unpub.) studied the development of vegetation filling up a pond, and Boardman (unpub.) examined an early stage of *Quercetum velutinae* following a burn.

Sere I

Allee (1934) has recently presented graphically an objectively correct outline of the succession of animal communities on an ocean shore. He takes into account the processes of erosion and deposit as they actually occur. His scheme for the Woods Hole, Mass., region fits admirably into the conditions of Long Island; we need only add the appropriate plant associations. It presents an extremely interesting contrast to the hypothetical—but still orthodox —scheme of Transeau. In Fig. 19 we have copied Allee's diagram completely, and inserted the corresponding plant association names.

Sere II

The associations of exposed sandy beaches and dune areas present such successional phenomena as Cowles (1899) described in his classic studies of Michigan dunes. But our dunes do not proceed to a truly wooded stage.

Cakiletum has no influence upon the substratum. It is followed by *Ammophiletum* whenever the sand is built up by wind and waves above the reach of any but the extreme storm tides. The coarse grass gathers sand on a windy shore and dunes result. So long as aggradation proceeds, *Ammophiletum* prevails. Back (to leeward) of the dunes, *Hudsonia tomentosa* prospers in stable areas enriched by a modicum of *Ammophila* humus. Or in arrested blowouts, *Hudsonia* establishes its association, and any trapped stalks of *Ammophila* perish. On Montauk Point, areas well stabilized and enriched by

Fig. 19. Diagram of littoral communities and seres. (After Allee).

Hudsonia are taken over by *Arctostaphylos uva-ursi,* and *Hudsonia* disappears. Blowouts deep enough to remain permanently moist are occupied by *Vaccinietum macrocarpi.* The margins of such depressions are often covered with *Myrica carolinensis.* On Fire Island a dwarf *Pinetum* (Assoc. 28) is found back of the dunes. It is possible that Pine Barren is the next step in such a sere. In places along the New Jersey shore this step seems certain. On Long Island there is no evidence that this has happened.

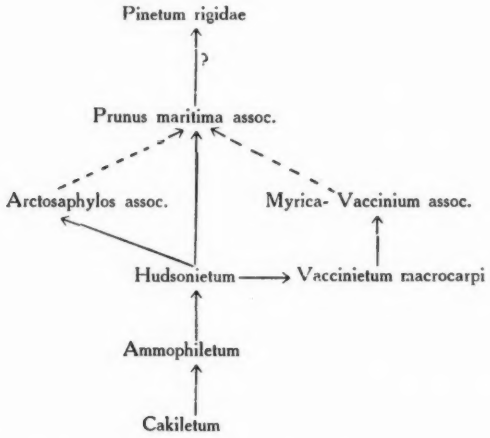

Fig. 20. Succession on aggrading sandy seashores.

Sere III

The inner harbor at the Laboratory, had in its deepest part, *Zosteretum marinae* followed in shallower water by *Ruppia maritima.* The harbor bottom has been raised by deposits of silt very much in the last century. Judging from Johnson & York's data, it cannot be doubted that the gradual filling of the harbor will make the water too shallow and temporary for *Zostera* or *Ruppia,* and *Ulvetum* will take their place. In like manner due to filling, *Spartinetum glabrae* is encroaching on *Ulvetum.* And this filling is aided by the silt-catching power of *Spartina* stands. Since the depth of the silt on the saltmarsh increases from the landward to the seaward side, it seems certain that *Spartinetum glabrae* has for centuries been marching seaward, followed by *Distichlidetum, Spartinetum patentis, Scirpetum americanae,* and *Thelypteretum.* Back of these, *Typhetum latifoliae* has come in since 1905, and is advancing seaward. No further step can at present be established. The fundamental factor responsible for the above sere was shown by Johnson & York to be the level of the land above (or below) mean low tide. This factor determines the length of daily exposure of soil and plants to salt water and to air.

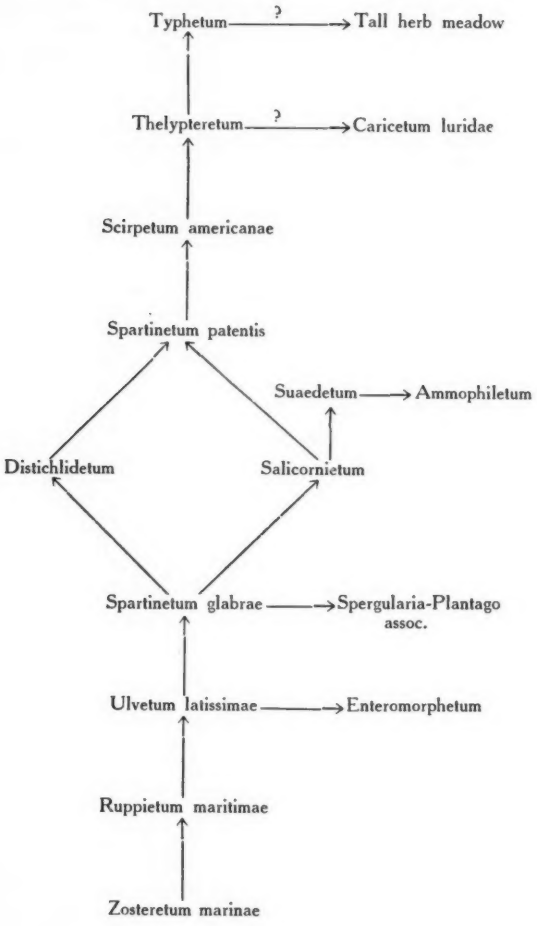

Fig. 21. Succession about the Inner Harbor.

An alternative progression is shown where a low sandy ridge separates an exposed shore from a protected sandy shore, as on the Sandspit, and east of Bayville. Here *Spartinetum glabrae* gives place to *Salicornietum,* and this to *Suaedetum,* while *Ammophiletum* crowns the ridge. Figure 21 shows these seres in diagram.

Second and third surveys of the saltmarsh near the Laboratory have shown an advance of *Thelypteretum* about 50 feet beyond its position in 1910. Part of this advance is by means of rhizomes, but a part seems to be by spores. Small isolated areas have appeared beyond the border; these increase in size and become confluent with the main bed of ferns. The advance of the fern is believed to be the expression of a change in the drainage of fresh water due to building a roadway across the head of the marsh in 1906. The appearance of *Typha latifolia* at the foot of the roadbank, and its spread, is due to the same cause. There is no evidence for change of level of the marsh, nor for any action of the plants themselves upon the habitat. Other saltmarshes round about are extremely stable communities. Those of Great South Bay and like localities are permanent until some change in the relative levels of the sea and land occurs.

The presence of buried stumps of trees *in situ* near the outer edge of the present saltmarsh at the Laboratory proves that the actual progression of vegetation in the past few hundred years has been from forest to saltmarsh!

Sere IV

At the head of III Lake, Kenney found *Caricetum strictae* with tussocks forming the first emersed vegetation. On this a shrub association takes root and comes to maturity. *Acer rubrum* finally comes to dominate the shrubs, as a humus layer 2dm. or more above water level is established, and *Aceretum rubri* results.

Aceretum rubri
↑
Swamp shrub Association
↑
Caricetum
↑
Pond muck without visible plants.

While this is bounded by *Quercetum,* there is no evidence whatsoever that *Quercetum* can survive, much less invade, on a peaty substratum. To extrapolate *Quercetum* as a stage beyond *Aceretum,* one must assume that the humus will be gotten rid of. Of course, if this happens, and if the water table is lowered, and if meantime the coast doesn't sink, or the sea rise, or the climate materially change, then at long last *Quercetum* will succeed *Aceretum.* Such a step is hypothetical (Br.-Bl., 1932). At Great River, *Aceretum* is already as near sea-level as trees can live. In upper New York State, a hill-country with possibilities of adequate drainage, mixed forest is said to occur on peaty soils (B. D. Wilson in litt.). Similar growth is reported from Michigan. Veatch in litt.).

Sere V

Since the vegetation of each pond is peculiar to itself, the seral relations are peculiar and individual. In the Pine Barren region, the zones have a seral relation if their vegetation can survive on the successive mineral or organic substrata. A pond filled by accumulation of peat will become a *Fruticetum* of *Vaccinium corymbosum* or *Azalea*, followed by *Aceretum*, or it will become a *Vaccinietum macrocarpi* with *Sphagnum*. In other regions, *Aceretum rubri* is the final stage on peat. Drainage of a pond, or filling with sand or gravel leads to the establishment of the neighboring major vegetation.

Sere VI

Abandoned agricultural land, of any kind, develops gradually to *Andropogonetum scoparii*. Denuded areas are likely to do the same. This is true in all of our area except the maritime portions. It is usual for *Juniperus virginiana* to become established in the grassland. Then, either by penetration from the border, or by appearance of isolated shrubs and trees, a *Quercetum* or an allied association ensues *(Liriodendretum*, fragmentary *Betuletum)*. (Cf. Blizzard, 1931). Decadent or dead *Juniperus* in woodland may be taken as certain evidence that the wood is on abandoned farm land. The usual influences of grass, shrubs and trees upon soils and microclimates occur on Long Isalnd, without any known peculiarities. The general climate is not such as to permit accumulation of peat except in waterlogged depressions.

Sere VII

Burns in Pine Barren

Quercetum ilicifoliae is the immediate result of fire in Pine Barren. It is also the result of celar cutting. If fire recurs, this association remains supreme. If fire is long kept out, *Pinetum* may return directly, as is seen west of Riverhead along Highway 25. It is commonly believed that *Quercetum velutinae* follows *Q. ilicifoliae* on Pine Barren. And probably this is the commoner way. In this case *Pinetum* is restored only after a very long time, if at all.

Sere VIII

Burns in Deciduous Forest

Mr. E. T. Boardman in 1927 studied an area of oak woods which was burned over in 1922. The fire lasted one day only. Four strips 2 x 10m. were selected for detailed analysis. *Quercus prinus* was present in two strips only. *Gaylussacia baccata* was in every strip, with a coverage on 1 x 2m. quadrats of 0 to 5. *Vaccinium vacillans* similarly graded 0 to 5, but was absent from one strip. *Quercus alba, Vaccinium pennsylvanicum, Lyonia mariana, Myrica asplenifolia* and *Pteridium aquilinum* were the only other species found in any considerable quantity on the strips. Mr. Boardman concluded that the oaks and ericads would have to furnish humus enough to enable other species to restore the original flora, and that this restoration would be hopelessly slow from an economic standpoint.

Sere IX—Denuded Areas

Conard's study of a denuded area in similar woodland had to do with an excavation for a railroad. After eleven years, numerous plants of the woods were re-established, but mostly from transplants. In 1930, and at the present time, there is an area of *Andropogonetum scoparii,* and thickets of small trees. The grass area had no surface humus or duff, the tree areas had about an inch of loose duff, and the upper two inches of earth was rich in humus. Earthworms were present. A considerable part of the area, however, was still entirely bare, or clothed with mosses: *Polytrichum commune, P. piliferum Ditrichum tortile vaginans.*

Old road or railroad banks become completely covered with the low shrubs and mosses of the adjacent wood. Taller vegetation is usually not allowed to remain.

Gravel slides along the Sound have often been recommended for study, but so far nothing suggestive has been discovered. The stabilization of slides is an economic problem on estates, and should be so considered along roadways and railroads. Horticultural methods for erosion control should be taken up. Preliminary observations emphasize the value of mosses in the earliest stages in shade or partial shade. *Polytrichum commune, P. juniperinum, Catharinea undulata, Ditrichum tortile vaginans, D. pallidum, Dicranella heteromalla* and even *Pogonatum brevicaule* and *Lophozia excisa* have been found retaining soil or preventing wash on a roadbank. On a very shady bank *Scapania nemorosa, Calypogeia trichomanes,* and *Nardia crenulata* have been found binding the surface (cf. Conard, 1935).

Part IV.—The Classification of Associations

According to physiognomy, Rübel (1930) has given an extensive classification, with descriptive diagnoses, of the known plant associations of the world. His terminology is avowedly incomplete in the treatment of aquatic plants. Land plants are divided into Lignosa and Herbosa; the latter heading is subdivided into Terriherbosa (on land), Aquiherbosa (in water), and Deserta. The last heading includes Siccideserta, Frigorideserta, Litorideserta, Mobiliderta, etc. Aquiherbosa include among a number of coordinate divisions "Enaliden" and "Salzwasser-Emersiherbosa." The terminology is incomplete. Rübel's scheme is extremely suggestive, but we have not been able to utilize it with entire satisfaction. For example, *Pinetum rigidae* would belong in Rübel's Aciculilignosa Aciculisilvae, and *Quercetum ilicifoliae* would belong in Aestilignosa Aestifruticeta, though they differ only in the more or less dense upper story of *Pinus* in the first, and the much denser growth of dwarf oaks in the second.

Based upon *the species which compose the associations,* we may group associations according to the similarity of the species lists (Braun-Blanquet, 1932, pp. 163-5). Thus similar associations form an Alliance (-ion), and similar Alliances an Order (-etalia). Similar orders may be grouped into a Class. On this basis, the associations so far studied on Long Island may be classified as in Table 4, following. The associations not listed in the table are not well enough known to warrant placing them in this classification. While that fact

TABLE 4

Alliances and Orders

Associations	Alliances	Orders
2. Laminarietum 3. Chondrus-Ceramium rubrum 4. Ahnfeldtia plicata 5. Dasya-Grinnellia 6. Polysiphonia 12. Ascophylletum 13. Fucetum 14. Rhizoclonium	Fucion	Fucetalia
9. Ulvetum latissimae 10. Enteromorphetum 11. Monostroma	Ulvion lactucae	
7. Zosteretum marinae 8. Ruppietum maritimae 59. Potametum 64. Nupharetum advenae	Potamion	Potametalia
15. Spartinetum glabrae	Spartinion glabrae	Spartinetalia
16. Salicornietum ambiguae 20. Suaedetum maritimae	Salicornion Br.-Bl. Thero-suaedion Br.-Bl.	Salicornietalia
17. Distichlidetum spicatae 18. Spartinetum patentis 21. Scirpus americanus	Juncion maritimi Br.-Bl.	Juncetalia maritimi Br.-Bl.
19. Spergularia-Plantago decipiens	Plantaginion crassifolii Br.-B.	
22. Cakiletum edentulae 23. Ammophiletum breviligulatae 24. Hudsonietum tomentosi	Ammophilion arenariae	Ammophiletalia Br.-Bl.
30. Phragmitetum communis	Phragmition Br.-Bl.	Phragmitetalia Br.-Bl.
31. Quercetum prini 32. Quercetum kalmietosum 33. Quercetum velutinae 34. Liriodendron 35. Fraxinus-Juglans	Quercion albae	Quercetalia albae
36. Betula lenta 37. Fagus grandifolia	Betulion albae	Betuletalia
28. Pinus rigida scrub 38. Pinetum rigidae 39. Quercetum ilicifoliae	Pinion rigidae	Pinetalia rigidae
40. Aceretum osmundaceum 41. Aceretum rubri	Acerion rubri	Aceretalia rubri
29. Vaccinietum macrocarpi 42. Vaccinietum corymbosi 43. Chamaedaphnetum calyculatae 68. Low shrub	Vaccinion corymbosi	Vaccinietalia
44. Chamaecyparetum thyoidis	Chamaecyparion	Chamaecyparetalia
45. Andropogonetum scoparii 46. Andropogonetum hempsteadi	Andropogonion scoparii	Andropogonetalia

indicates a certain inadequacy of the scheme, it also shows the advantages of a scheme which demands extensive and minute knowledge of associations before they can be properly placed. This is as it should be.

For purposes of comparison and correlation of diverse associations within a single phytogeographic region, this is the best device yet proposed. The species lists are comparable.

The table shows that one cannot assume that two associations named from the same taxonomic genus are related. *Spartinetum glabrae* is allowed an Alliance and an Order of its own. *Spartinetum patentis* belongs in *Juncion maritimi*, and the order *Juncetalia maritimi*. As to floristic composition and social relations, the two *Spartineta* are very distinct. The same will be true of *Pineta*, *Querceta*, and many other associations whose major species belong to large and widely distributed taxonomic genera. An illustration may be drawn from three *Querceta* described above.

TABLE 5

Comparison of species lists from one quadrat in each of three *Querceta*.

	Total Vascular plants	V. pl. peculiar to this assoc.	Total mosses	Mosses peculiar to this assoc.	Vasc. pl. in 1 and 2	Vasc. pl. in 1 and 3	Vasc. pl. in 2 and 3	Vasc. pl. in all three	Mosses in 2 and 3
Pinetalia Pinion rigidae 1. Quercetum ilicifoliae	28	17	4	4	4	3		4	
Quercetalia Quercion albae 2. Quercetum velutinae	22	4	11	1	4		10	4	10
3. Quercetum kalmietosum	40	23	19	9		3	10	4	10

Table 5 presents an analysis of the species lists of three *Querceta*. It is found that *Q. ilicifoliae* has only 8 species of vascular plants in common with *Q. velutinae*, and 7 with *Q. kalmietosum*, whereas the last two have 14 species in common of which 4 are common to all three. Fourteen species represent 35% of the total number of vascular species in *Q. kalmietosum*, and 63% of those in *Q. velutinae*. The mosses &c. of *Q. ilicifoliae* are all peculiar to it. In the other *Querceta* there are ten species of mosses, &c., common to both, being 90% of the species of this class in *Q. velutinae*, and 53% of those of *Q. kalmietosum*. The two arborescent *Querceta* are thus much more closely related than is either one to the scrub-oak association.

But Alliances and Orders, based on species, give no clue to the similarities in organization of widely separated communities with no species in common. Such comparisons were attempted, on both local and worldwide scales, by Raunkiaer, through the medium of Life Forms. Taylor (1918) has made a

study of the Raunkiaer life forms of the Long Island flora. He presents the following table:

	MG	MS	MC	N	Ch	H	G	HH	T
Normal spectrum	6		17	20	9	27	3	1	13
Local flora	.52	4.03	7.18	3.51	5.29	33.29	20.23	11.74	13.00
Total L. I. flora	.89	4.37	6.34	2.77	5.89	33.15	20.10	10.90	13.94
400 commonest L. I. species	1.50	3.00	8.50	4.25	7.25	30.00	21.00	6.75	14.25

Local flora means the "whole region near New York" presumably from Taylor's Flora. The total Long Island flora consists of 1120 native plants. Taylor concludes that in actual fact the spectrum for Long Island plants is more nearly "normal" for the whole world than is Raunkiaer's "normal spectrum."

On the basis of *sociological simplicity or complexity*, Braun-Blanquet (1928, 1932) has proposed an extensive classification of communities, proceeding from very simple communities without competition, (plankton), to many layered communities with a multitude of social relations. Table 6 follows this scheme. It is excellent for showing degrees of social complexity, and can be used for comparisons of social relations on a worldwide scale.

TABLE 6

Associations arranged according to sociological complexity (numbers refer to Associations described above)

A. Extra-regional communities.
Plankton of bays, Sound and sea: 1.
Euglena ponds: 51.

AA. Regionally delimited layered communities.

B. One layered communities without root competition.

C. Floating
Lemna-Spirodela association.

CC. Attached
Epixylic communities of lichens and mosses.
Parmelia, Physcia, Graphis
Frullania, Orthotrichum, Platygyrium
Rock or soil communities
Submersed algal and moss communities
2. Laminarietum
3. Chondrus-Ceramium rubrum association
4. Ahnfeldtia association
5. Dasya-Grinnellia Association
6. Polysiphonia association
9. Ulvetum latissimae
10. Enteromorpha association
11. Monostroma association
12. Ascophyllum association

13. Fucetum
14. Rhizoclonium association
55. Moss pond on High Hill
Drepanocladus; Fontinalis
Communities of soil algae, lichens and mosses.
Baeomyces roseus communities
Riccia Sullivantii communities
Anthoceros-Blasia communities
Polytricheta as parts of major communities
Sphagneta

BB. Two or more layered communities with root competition
D. Open communities
Two layered
7. Zosteretum marinae
8. Ruppietum maritimae
16. Salicornietum ambiguae
19. Spergularia-Plantago decipiens association
20. Suaedetum maritimae
45. Andropogonetum scoparii
47. Chrysosplenium americanum association
48. Radicula-Callitriche association
53. Extinct pond
54. Clear pond on High Hill
58. Gratiola-Hypericum association
59. Potametum
61. Sparganietum
63. Caricetum strictae
64. Nupharetum
65. Eriocaulonetum
69. Portulacetum
Three layered
22. Cakiletum edentulae
23. Ammophiletum breviligulatae
26. Juniperus virginiana beach association
73. Plow land
75. Paths and wagon tracks

DD. Closed communities
EE. Without shrubs or trees
15. Spartinetum glabrae
17. Distichlidetum spicatae
18. Spartinetum patentis
21. Scirpus americanus association
30. Phragmitetum communis
46. Andropogonetum Hempsteadi
49. Tall herb association of wet meadows
50. Carex lurida association
51. Thelypteretum
56. Polygonum pond
57. Decodon pond
60. Typhetum
66. Cyperus dentatus-Juncus dichotomus association
67. Agrostidetum hyemalis
70. Lawns
71. Mowing fields
72. Pastures
EE. With woody plants
F. With shrubs, without trees

24. Hudsonietum tomentosi
25. Prunus-Myrica association
27. Iva-Baccharis association
28. Pinus rigida scrub association
29. Vaccinietum macrocarpi
39. Quercetum ilicifoliae
43. Chamaedaphnetum calyculatae
62. Fruticetum at head of III lake.
68. Low shrub association of wet pine barrens
74. Slash land

FF. With trees

31. Quercus prinus association
32. Quercus prinus association with Kalmia
33. Quercus velutina association
34. Liriodendron association
35. Fraxinus-Juglans association
36. Betula lenta association
37. Fagus grandifolia association
38. Pinetum rigidae
40. Aceretum osmundaceum
41. Aceretum rubri
44. Chamaecyparetum thyoidis

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THE VEGETATION OF PINE MOUNTAIN, KENTUCKY:

AN ANALYSIS OF THE INFLUENCE OF SOILS AND SLOPE EXPOSURE AS DETERMINED BY GEOLOGICAL STRUCTURE

E. LUCY BRAUN

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I.—Introduction

The vegetation of Pine Mountain stands out in strong contrast to that of the rest of the Cumberland Mountains. In the midst of a luxuriant deciduous forest region the long, though broken, strip of pine forest cannot but attract attention. In fact, the name of the mountain is itself a reflection of its distinctive vegetation. Such a strong local contrast at once suggests that here edaphic factors are in control. An opportunity is afforded to consider their effectiveness in overcoming the major climatic factors.

The average annual rainfall is about 45 inches, fairly evenly distributed throughout the year; there is usually some precipitation on about one-third of the days. The temperature ranges from an average January minimum of about 25° F. to an average July maximum of about 87° F. Extremes range from below zero to above 100°.

II.—Geology and Topography of Area

The Cumberland Mountains constitute a small section of the Appalachian Plateaus Province (Fenneman, 1928) in extreme southeastern Kentucky and extending some fifty miles southward into Tennessee and fifteen or twenty miles eastward into southwestern Virginia. Pine Mountain, formed by the Pine Mountain thrust fault, extends 125 miles in a northeast-southwest direction from West Virginia into Tennessee; in a part of its Kentucky extent it forms the western border of the Cumberlands. It is a monoclinal mountain, its strata dipping southeastward, their jagged and broken upturned edges forming the mountain crest (Figs. 1 and 14). The strong Lee conglomerate (Pottsville) is turned upward, determining in general the slope of the southeast face of the mountain, and forming the resistant summit which overhangs and protects from erosion the weaker strata outcropping on the north or northwest face of the mountain. Hence the south or southeast face is a relatively

gentle slope,—the dip of the strata; the north or northwest face excessively steep,—the eroded edges of strata.

The dip slope of the mountain averages about one and one-half miles in length, rising in that distance some 1200 or 1500 feet. The steeper scarp slope in many places drops 1000 feet in three-eights of a mile and locally that much in a quarter of a mile. The crest of the mountain ranges in elevation from 2500 to 3200 feet. It is formed by the lowest resistant member of the Pottsville; successively higher strata (stratigraphically) whose edges do not attain the summit form longitudinal ridges or humps, commonly called "false summits," on the southeast face of the mountain (see diagram, Fig. 1). Interbedded weaker strata have yielded to erosion and in profile (Fig. 1) appear as dips or concavities in the slope; actually they are troughs paralleling the strike of strata.

The dip slope is indented by many permanent streams roughly parallel and usually only one-half mile to a mile apart which drain into the Poor Fork of the Cumberland River (in the area discussed). These receive minor tributaries at right angles (usually not shown on topographic maps) which drain the longitudinal troughs on the weaker strata. Deep gorges cut in the sandstone vary in character in relation to the angle which the stream makes with the dip. In places overhangs or "rockhouses" result. Falls of greater or less height are general; the falls of Bad Branch, 60 feet in height, are produced by a stream flowing at an angle to the dip. In such streams, the most sheltered gorges occur. While all of the streams of the dip slope are southerly flowing streams, many in places are so narrow and so protected from direct sun as to support very mesophytic vegetation, generally a mixed forest with hemlock and Rhododendron.

Streams are few on the steep north-northwest face of Pine Mountain; in one stretch of thirty miles there is none large enough or permanent enough to appear on topographic maps on scale of one inch to a mile. The even slope is interrupted only by shallow concavities down which at times some water trickles and the intervening convexities which in places are accentuated by huge mounds of debris reminiscent of former slumps.

At the foot of Pine Mountain on the southeast, in the area under consideration, is the Poor Fork of the Cumberland River, flowing in a deep longitudinal valley. To the east of it rises Black Mountain, attaining elevations 1000 feet in excess of Pine Mountain, and clothed throughout with deciduous forest, interrupted only by hemlocks on its lowest slopes. To the northwest of Pine Mountain is deeply dissected plateau country, its highest summits near to Pine Mountain being 500 to 1000 feet lower than Pine Mountain; it also is almost entirely deciduous forest covered in this area. The crest of Pine Mountain stands boldly above everything to the west. Several small longitudinal valleys skirt the immediate northwest base of Pine Mountain, each in turn soon assuming a winding course westward through the plateau toward the Kentucky River (in the area under consideration).

The mountain, then, is seen to rise rather abruptly from valleys on either

Fig. 1. Generalized profile of Pine Mountain. Longitudinal ridges or humps are indicated by Roman numerals, longitudinal troughs by letters. The diagram shows geological structure and lithological character of rocks. Numbers (1 to 23) below the profile refer to areas crossed by profile and correspond to paragraph numbers in text. A stream profile (starting near *f* and sloping rapidly downward) is shown within the mountain profile. Divisions of the stream as treated in the text are numbered from *R1* to *R5*.

side to an irregular summit notched by shallow gaps but unbroken by water gaps from the Breaks of Sandy southeast of Pikeville to the Cumberland River gap at Pineville, a distance of some hundred miles by mountain crest. Throughout this entire extent, the structural, topographic, and vegetational features are similar. The specific features of vegetation described and the correlations made are based on observations on Pine Mountain in Harlan and Letcher counties between Pine Mt. Post Office and Bad Branch near the headwaters of the Cumberland, and especially from studies in the vicinity of Partridge, Letcher County.[1]

Every change in lithological character of the rock results in change in topography and in soils and is reflected in the vegetation. While Pine Mountain as a whole stands out in contrast to its neighbor mountains, it is itself marked by extreme vegetational contrasts within short distances—50 or 60 feet.

The accompanying profile of Pine Mountain near Elkins Branch (Fig. 1) is representative of areas between streams. The angle of slope in places approximates the dip of strata; in other places bevels the upturned ends of strata. At such humps as *II*, *III*, *V*, and *VI*, formed by resistant strata, rock is exposed, presenting on the one side, the dip slope, a smooth stratum surface (Figs. 4 and 8); on the other, the scarp slope, a steep or cliff-like exposure (Fig. 7). Less resistant strata (as at *I*) or strata not separated by erosion troughs from adjacent resistant layers (as at *IV*) may be soil covered. Troughs or flats appear on weaker strata (indicated by letters on the profile). The trough nearest the mountain summit (*f* on profile) is everywhere the deepest and most pronounced. It is usually occupied by sluggish streams with here and there swampy patches. At the mountain crest (*VII*), which is sometimes but little higher than the last false summit from which it is separated by the pronounced trough, sandstone again is exposed (except in gaps), forming on the scarp side, bold cliffs (Figs. 14, 15). The scarp slope of Pine Mountain bevels the edges of strata stratigraphically lower than the basal sandstone member of the Pottsville (exposed at *VII*); it is everywhere steep, held up by the summit cliff. The slope is fairly uniform, although about one-half to two-thirds of the way up a limestone ledge (*VIII*) sometimes outcrops, forming low cliffs.

Soils are derived from the underlying rock and where shallow clearly reflect the character of the rock. Thus over much of the dip slope, sandy soils prevail. These are interrupted in some of the flats and troughs by clayey or sandy-clayey soils. The soil at *f* is clay. On the northwest face of the mountain soils are deeper and except at the summit and locally at the limestone cliff show no apparent relation to underlying rock. Fragments of rock from the sapping back of the cliff above are everywhere, forming a considerable part of the "soil" volume. Specific features of the soils at intervals on both slopes will be given in connection with the discussion of the plant communities.

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1 Most of the area is covered by the Whitesburg and Nolansburg topographic sheets.

III.—Plant Communities

The plant communities of Pine Mountain are treated in four sections: (A) the southeast or dip slope, (B) the summit, (C) ravines of the dip slope, (D) the northwest slope. The general sequence of plant communities, the relation of communities to specific outcrops and to soils, and contrasts between communities are sufficiently alike throughout the area observed that any one sequence may be taken as representative. Hence transects of communities along the line of the profile and along a stream are used to demonstrate composition and contrast of communities. Areas crossed by the profile are indicated by numbers below the profile. Each area is to be though of as a band parallel to the mountain base or summit, and varied laterally by slight concavities or convexities (ridges); ravines transverse to the outcrops cannot be indicated on the mountain profile. A stream profile is shown within the slope profile (Fig. 1).

Definitive terms, such as association and climax, are avoided in the descriptive section of this paper, III, so that the discussion may not be encumbered by previously conceived ideas of status of the communities.

For the sake of brevity and convenience in the text, trees are referred to by common names. A list of common names used and corresponding scientific names[2] may be found in the table of forest types, section IV. Scientific names of shrubs, and sometimes of herbaceous plants, are not repeated in the text when the generic name alone clearly refers to a plant previously mentioned; for example, *Kalmia latifolia* is usually referred to as Kalmia.

A.—The Southeast or Dip Slope

1.[3]—The lowest slopes vary considerably from place to place. Remnants of higher strata sometimes form additional lower knobs where the base of the mountain projects farther east (where the river is close to Black Mountain); or the prominence of knob *I* is lessened where the river cuts the slopes of Pine Mountain. In general, the lowest slopes are white oak-beech or a mixed forest of oaks and chestnut[4] with a small percentage of beech, tulip and red maple, varying to beech-white oak-red maple or a mixed mesophytic forest of beech, basswood and tulip on northerly exposures. The undergrowth is usually poor, containing *Polystichum acrostichoides, Smilacina racemosa, Anemonella thalictroides, Heuchera* sp., *Sedum ternatum* and *Chimaphila maculata.*

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2 The nomenclature used is, with few exceptions, that of Gray's New Manual of Botany, 7th edit., 1908.

3 Paragraph numbers correspond to area numbers below the profile, Fig. 1.

4 Throughout this paper, dead and dying chestnut trees, as well as living ones, were counted for composition lists, for in this section the mortality was not high until the last few years. Only in this way was it felt that a true picture of original composition could be gained.

2.—An admixture of pine enters on low ridges, and the forest composition[5] is:

chestnut	37%	red oak	4%
white oak	33	scarlet oak	4
yellow pine	8	hemlock	4
pitch pine	8		

On these low ridges a heath understory of *Kalmia latifolia, Vaccinium stamineum, Azalea calendulacea, Gaultheria procumbens, Epigaea repens* prevails with *Cypripedium acaule, Lespedeza hirta, Gerardia (Dasystoma) laevigata, Lobelia puberula, Aster undulatus* (Fig. 2). The soil in this low ridge-top community is covered by a thin mat of humus (duff),[6] beneath which is a podsolized layer (A horizon) about one inch in thickness (pH 4.74) grading down to yellow sandy soil (pH 4.66). On the flattest areas the duff is thicker, the podsolized layer is almost lacking (pH 4.32) and the soil below slightly more acid (pH 4.32).[7] In the most pronounced Kalmia heaths of these sandy shale slopes, the duff is differentiated into an upper matted leaf duff (pH 4.15) and a lower gray fibrous duff with abundant mycelia (pH 3.98); the A horizon (pH 3.98) is more acid than the yellow soil beneath (pH 4.83).

3.—On sandy shaley slopes rising above these oak-heath ridges a mixed oak forest prevails; heaths continue, together with a larger admixture of other plants as *Castanea pumila, Pogonia verticillata, Potentilla pumila, Cassia nictitans, Gentiana decora, Gentiana villosa, Houstonia tenuifolia, Campanula divaricata, Erigeron pulchellus, Sericocarpus asteroides, Chrysopsis mariana. Cunila origanoides* is characteristic of more open places; the lichen, *Baeomyces roseus*, pioneers on bare areas, and *Viola pedata* is an early invader.

4.—The influence of an underlying sandstone becomes apparent in the much sandier soil. While there is no pronounced change in forest, the admixture of pines, apparent only on knobs and ridge tops lower down, is important. The forest composition is:

chestnut	42%	white oak	8%
red maple	10	scarlet oak	5
chestnut oak	10	yellow pine	3
pitch pine	10	black oak	1.5
tulip	8	pignut hickory	1.5

The heath understory continues with Kalmia dominant and a lower heath layer of *Epigaea, Galax aphylla,* and *Gaultheria.* In places, a secondary

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5 Composition, in percentages, is given only when the forest stand is primary or near enough so that the figures were thought to be representative of primary conditions.

6 Duff and mull as defined by Romell and Heiberg, 1931.

7 pH values determined electrically with quinhydrone electrodes; air-dried soils used in all cases.

effect due to dead or dying chestnut is reflected in increase in pine; elsewhere under dead chestnut, the young deciduous species have made such a dense stand that the heath understory is reduced. A varied herbaceous layer contains *Pteris aquilina, Andropogon scoparius, Hypoxis hirsuta, Clitoria mariana, Baptisia tinctoria, Desmodium rotundifolium, D. laevigatum, Lespedeza* spp.,

Fig. 2. Chestnut-white oak forest of area 2. Due to dying chestnut, more light admitted than formerly. *Kalmia latifolia* important in the heath understory.

Tephrosia virginiana, Viola pedata, V. sagittata, Ascyrum hypericoides, Gentiana villosa, Solidago bicolor, Coreopsis major, and a few species more characteristic of sandy soils as *Aletris farinosa, Chrysopsis graminifolia* and *Solidago odora.* These herbaceous plants, which throughout the area are generally confined to sandy soil, appear for the first time in this area although the soil reactions show no essential change in acidity. A layer of duff 1 to 2 inches deep covers the ground surface; beneath is 1 to 2 inches of white tough podsol (pH 4.15) and then fine yellow sandy soil (pH 4.49).

A common variation at this horizon is due to ascending ridges (convexities of slope) which are very rocky. These cannot be shown on the profile. The soil accumulated between rocks is more acid than on the slope (pH 3.81 and 3.98), generally pale and sandy. The forest of such ridges *(4a* of table in section IV) is always dominantly chestnut oak (Fig. 3):

chestnut oak	56%	scarlet oak	3%
chestnut	18	white oak	1.5
pitch pine	8	red maple	1.5
yellow pine	5	tulip	1.5
black oak	3		

The undergrowth is made up of the same species and dogwood, Sassafras, sourwood and service berry. Heaths, including *Kalmia, Vaccinium vacillans, V. stamineum, Gaultheria, Galax* and *Epigaea,* are abundant but do not form a continuous layer. The herbaceous plants are essentially as noted for the general slope.

Higher, in the upper part of area *4 (4b* of table), the soil is more shallow. This is reflected in an increase in pine to one-fourth or more of the canopy:

chestnut	32%	scarlet oak	12%
chestnut oak	20	tulip	5
yellow pine	15	black oak	2
pitch pine	12	sour gum	2

Chinquapin *(Castanea pumila)* is more abundant here than at any other horizon, except parts of the lowest slopes. Duff formation is less pronounced: there is no podsol, instead some gradation from humus to mineral soil (pH 4.32 to pH 4.83).

The upper part of the sandstone stratum whose slope is included in area *4* may give rise to a flat ridge top (on certain narrow areas between streams) on which a fairly deep soil has accumulated. In such locations an oak or oak-chestnut forest *(4c* of table) develops in which white oak is an important species:

chestnut	36%	black oak	3%
white oak	17	pitch pine)	3
chestnut oak	13	yellow pine)	
scarlet oak	13	sour gum)	3
red maple	6	sourwood)	
tulip	6		

The understory is open; a few heaths are present including *Kalmia, Rhodo-*

dendron maximum and flame azalea *(Azalea calendulacea);* herbaceous plants are few. The surface of the ground is covered by a heavy oak litter decomposing into a one inch layer of brown fibrous duff; beneath this the A horizon of about 1 inch is gray and spongy (pH 4.32); at 5 inches the pH value is 5.00.

Fig. 3. Chestnut oak community of ascending ridges, area 4. Note the tall straight form of this species in deep soil and contrast with Fig. 9.

5.—Where a longitudinal ridge is formed (parallel to the mountain axis) as indicated by the profile at *II*, the vegetational response is more striking. The sandstone outcrops and a stratum surface dipping at an angle of 30° is presented on the mountain face (Fig. 4). This is occupied by *Umbilicaria pustulata, Parmelia, Physcia,* and various crustose lichens. Mats of *Cladonia, Hedwigia* and *Grimmia* follow (Fig. 5). The only herbaceous plant is *Corydalis sempervirens.* Creeping up the rock surface from the accumulated mat of pine needles collected along the edge of the soil covering, Gaultheria forms extensive mats. Clumps of *Gaylussacia baccata* appear wherever soil has accumulated to a depth of one to eight inches (Fig. 5). The pH value of this soil is 3.9 to 3.98. Wherever a deeper soil accumulates, red maple, sour gum, sourwood and service berry invade. *Vaccinium vacillans* enters later. Yellow pine comes to within a few feet of the soil edge. A pine belt of yellow and pitch pine everywhere borders the rock outcrop or follows the very shallow soil which covers it (Fig. 6). This pine belt, almost continuous along the mountain except as interrupted by ravines is apparent from the valley below. Where only one to two feet of soil have accumulated, yellow pine prevails; where the soil is slightly deeper, pitch pine mingles with yellow pine and deciduous species begin to enter. Under pines where needles accumulate, the lichen-moss vegetation is eliminated. The shrub layer on the patchy soil layer over the sandstone contains *Gaylussacia, Vaccinium, Pyrus melanocarpa, Rhus copallina, Castanea pumila* and a few small trees (Figs. 5, 6).

Where cut across by streams this sandstone ledge forms high cliffs in the crevices of which are *Kalmia, Rhododendron* and *Vaccinium corymbosum.*

6.—A sharp vegetational contrast is produced where the scarp slope of this sandstone drops down into a shallow trough (Fig. 7). Pine drops out; chestnut assumes the form and proportions usual in mesophytic forest areas. The forest composition is:

chestnut	50%	red oak	6
chestnut oak	22	white-heart hickory	3
tulip	16	mountain magnolia	3

The understory is of saplings together with shrubs *(Rhododendron, Clethra acuminata, Pyrularia pubera, Hamamelis virginiana, Rubus alleghenensis),* wild grape *(Vitis bicolor)* and mountain magnolia. The aspect is much more mesophytic due to the absence of pines, to fewer ericads and more deciduous shrubs in the understory. Ferns—*Osmunda cinnamomea, Aspidium noveboracense, Polystichum acrostichoides* and *Dicksonia punctilobula*—add to the mesophytic aspect. Other herbaceous mesophytes include *Medeola virginiana, Aristolochia Serpentaria, Desmodium grandiflorum, D. laevigatum, D. paniculatum, D. canescens, Phaseolus polystachyus, Viola hastata, Asclepias phytolaccoides* and *Elephantopus carolinianus,* most of which do not occur in the slope forests. The drop from the sandstone crest into this trough is only 10 to 25 feet. A deeper and less acid soil (near surface, sandy humus, not duff, pH 5.5; deeper, dark brown sandy earth, pH 5.17), and topography permitting of more soil moisture throws the balance of factors in favor of de-

Fig. 4. Upper edge of first longitudinal ridge, at *II* of profile. Picture shows dip surface of a sandstone stratum with well established lichen vegetation. To the left is mesophytic forest of trough *b*.

Fig. 5. Mats of *Cladonia* and *Hedwigia* on outcropping sandstone stratum (area 5) and shrub invasion.

Fig. 6. Yellow pine-pitch pine community on shallow soil over sandstone. *Castanea pumila* in bloom in foreground. This is but a few feet from area shown in Fig. 5.

Fig. 7. Scarp slope of first sandstone outcrop *(II)* and trough, *b*. Large chestnut trees formerly made up about half of this forest community. *Rhododendron maximum* and ferns add to the contrast in appearance and floristics between this community and the ones immediately adjacent to the left which are shown in Figures 5 and 6.

Fig. 8. The dip slope of the resistant sandstone stratum which forms the prominent ridge crest at *III* on profile here faces southeast. The lichen→pine succession of area 8 which is diagrammed in Fig. 10 is illustrated here. *Pinus virginiana* the important tree.

ciduous forest with deciduous understory. This trough is never pronounced and sometimes is entirely absent; the slope ascends almost at once over another sandstone.

7.—Area *7* supports a typical sandy soil slope vegetation; convex portions of the slope are occupied by chestnut oak forest essentially as in area *4:*

chestnut oak	60%	scarlet oak	2.5%
chestnut	15	sour gum	2.5
white oak	7	yellow pine	2.5
red maple	5	pitch pine	2.5

The heath layer is prominent; *Solidago odora, Aster linariifolius* and *Polygala Curtissii* are important. The soil contains a large amount of white quartz sand and pebbles.

8.—The second false summit at *III* of the profile is generally more prominent than the first. The rock is a conglomeratic sandstone, very resistant. Earlier stages of the rock surface succession are better represented and the succession more complete, culminating in a pine-chestnut oak forest (Figs. 8, 9). The succession is represented by Fig. 10; the canopy composition of the ultimate stage present is:

scrub pine	21 } 34%	red maple	8%
pitch pine	13 }	sour gum	5
chestnut oak	26	sourwood }	5
chestnut	13	mountain magnolia }	
scarlet oak	8		

Fig. 9. The open pine-chestnut oak community of the ridge crest at *III*. Note the gnarled form of the large chestnut oak *(Quercus montana)* to the left, the characteristic form assumed in shallow soil over rock. This form contrasts strongly with that shown in Fig. 3.

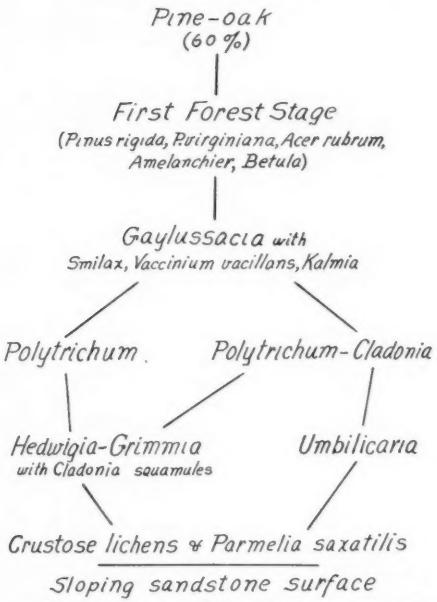

Fig. 10. Diagram of succession on sandstone of ridge crest at *III*.

Under trees of the open pine-oak forest is a mat of sandy humus supporting cushions of *Polytrichum, Dicranum, Catharinea* and *Leucobryum*. Where there are heath shrubs in these mats, leaves accumulate and the mosses die. Where there is a ground layer it includes heath shrubs—*Gaylussacia baccata, Vaccinium vacillans, Kalmia, Gaultheria, Epigaea* and *Galax*—and a few other plants as *Tephrosia, Chrysopsis graminifolia, Danthonia sericea, Smilax glauca* and *Mitchella repens*. The ground is covered with a pine-oak-Kalmia leaf litter, beneath which is about one inch of fibrous duff; next a ½-1 inch layer of pale fibrous sandy soil (pH 3.9) and then light yellow sand (pH 4.57).

9.—A drop of 35 feet in 60 feet from the open dry pine summit into an east-west trough *(c)* results in another of the sharp vegetational contrasts so conspicuous on Pine Mountain. The steep scarp slope, facing north, supports a shrub thicket of Rhododendron, Kalmia, red Azalea,[8] Clethra and dogwood. The trough itself is mesophytic (Fig. 11). A stream starts in a Kalmia-Rhododendron-alder thicket with *Osmunda regalis, O. cinnamomea, Aspidium noveboracense, Glyceria nervata, Scirpus atrovirens, Carex* spp.,

8 This Azalea is distinct from *Azalea calendulacea* in time and habit of blooming and in habitat. It will be referred to throughout this paper as "red Azalea." Noted in Small (1933) under *A. calendulacea* as possibly distinct.

Sagittaria latifolia, Juncus effusus, Habenaria sp., *Boehmeria cylindrica* and *Chelone glabra.* The trees of the trough forest are tall and straight in contrast to the low broad crowns of the ridge tops. The forest composition is:

chestnut	27%	sour gum	10%
white oak	20	chestnut oak	7
tulip	20	sourwood	7
red maple	10		

A tall shrub or small tree layer includes *Acer pennsylvanicum, Hamamelis, Pyrularia, Viburnum acerifolium, Cornus florida* and a few ericads—*Rhododendron, Vaccinium pallidum, Kalmia* and red Azalea. The herbaceous plants are mesophytes of acid woodlands: ferns *(Aspidium noveboracense, Polystichum acrostichoides, Osmunda Claytoniana), Panicum* spp., *Medeola virginiana, Clintonia umbellulata, Pogonia verticillata, Epipactis pubescens, Viola hastata, Desmodium* spp., *Chimaphila, Galax, Solidago monticola* and *Hieracium paniculatum.* The soil is clayey and less acid than on the slopes (pH 6.18 at one inch depth and pH 5.41 at 5 inch depth).

10.—Again the slope rises and the soil is sandy. The forest at first is oak-chestnut, with large and stately chestnut oak:

chestnut oak	47%	tulip	7%
white oak	18	sourwood	5
chestnut	20	sour gum	3

The forest of these slopes varies from oak-chestnut to oak-pine, locally pine; chestnut oak in the oak-pine community is stunted and crooked (see Fig. 9). *Gaylussacia* and *Vaccinium vacillans* are prominent in the heath layer.

11.—The fourth crest *(IV)* is usually not prominent; the forest is mostly chestnut oak and scattered pine in open stand with heaths, *Andropogon scoparius, Scleria triglomerata, Pteris, Chrysopsis graminifolia, C. mariana* and *Solidago odora.* Where rock is covered by only an inch or two of soil Gaylussacia prevails.

12.—A shallow trough may follow this outcrop. The forest reflects the deeper soil in the complete absence of pine.

13.—The next rise is usually steep with sandstone outcropping in places on the surface of the rise. Chestnut oak and pines are dominant with a heath understory in which Vaccinium and Gaylussacia are most important.

14.—At *V* and *VI* on the profile the upturned edges of resistant and massive sandstones make a pronounced crest or double crest, which in places equals the mountain summit in elevation. The forest here is open, generally 50 per cent or more pine (Fig. 12):

pitch pine	46} 56%	scarlet oak	6%
yellow pine	10}	black oak	6
chestnut oak	19	sour gum	3
chestnut	7	sourwood	3

Fig. 11. Mesophytic forest of trough c in area 9 which is less than 100 feet from the pine-lichen communities of Fig. 8. The trees here are tulip (left) and sour gum (right) with large chestnut between and beyond. Red maple, white oak and tulip in background. The contrast between this forest and that shown in Figs. 8 and 9 is evident even in pictures.

The understory is similar with such additional species as Sassafras, red maple, persimmon, service berry and on the scarp margin, mountain magnolia. An open shrub layer — dependent on soil accumulation — consists of *Gaylussacia baccata, Vaccinium vacillans, V. stamineum, Pyrus melanocarpa, Smilax Bona-Nox* and *Rhus copallina.* The herbaceous growth is varied though sparse, made up largely of sun plants; it includes *Sorghastrum nutans, Andropogon scoparius, Danthonia sericea, D. spicata, Tephrosia virginiana, Lespedeza repens, Ascyrum hypericoides, Aureolaria (Dasystoma) pedicularia austromontana, Eupatorium verbenaefolium, Aster surculosus, A. patens, A. linariifolius, Chrysopsis graminifolia, C. mariana, Sericocarpus asteroides, Helianthus divaricatus, Coreopsis major* and on almost bare rock, *Corydalis sempervirens.* Where soil has not accumulated a typical sandstone rock surface vegetation is seen with *Hedwigia* and *Cladonia* mats; the rock surface vegetation is not, however, as important as on the ridge at *III* of the profile.

15.—Immediately over the edge of the crest, the aspect changes greatly. The upper half of the scarp slope supports a dense heath shrub layer about five or six feet in height, made up mostly of *Kalmia,* with *Vaccinium corymbosum, Gaylussacia baccata, Azalea calendulacea* and *Rhododendron maximum.* Beneath the taller shrubs is a lower less continuous layer of Vaccinium and Gaylussacia, and a ground layer of Gaultheria, Epigaea and Galax. The aspect is that of the heath balds of the Great Smoky Mountains, though the area of course is small. The layer of Kalmia duff is 1-3 inches deep (pH 3.98); a pale gray sandy layer (pH 4.06) beneath is about 2 inches deep, and below is yellow sandy-clayey soil (pH 4.23).

About one hundred feet (vertically) down the slope the heath layer opens up and more herbaceous plants enter including *Cypripedium parviflorum, Steironema tonsum, Solidago caesia, Aster divaricatus* and *Prenanthes serpentaria.* Here the layer of duff is less pronounced, about 1-2 inches in thickness. The pale layer is lacking; a yellow sandy soil (pH 4.4) immediately underlies the duff and grades down to a yellow clayey material (pH 4.3).

Where the trough, *f,* is not cut so deeply the heath layer occupies both slopes of the trough forming an understory in a chestnut oak-chestnut forest. No change to the type of vegetation described for area *16* takes place.

16.—The trough, wherever cut more deeply, supports some type of mesophytic forest. In the area crossed by the profile the trough is 200 feet deep, the deepest part only about 600 feet from the crest of the scarp slope. The heath layer drops out rather abruptly about half way down the scarp slope. The whole aspect is that of rich mesophytic woodland (Fig. 13). The forest varies considerably in composition from place to place but everywhere chestnut and tulip are important, sometimes forming as much as 50 per cent of the stand; in addition are chestnut oak, beech, red maple, red oak, pignut hickory, walnut, basswood, cucumber tree, birch and sour gum. The varied understory includes these species and dogwood, mountain magnolia, striped maple, and sometimes hemlock. Shrubs are numerous, including *Hydrangea arborescens.*

Fig. 12. Pine forest of ridge crest *V* (area *14*) with open heath layer.

Rubus alleghaniensis, Pyrularia, Viburnum acerifolium, Hamamelis, Clethra, Benzoin aestivale, the late blooming red Azalea which takes the place of *Azalea calendulacea* of heath communities, and tangled masses of *Aristolochia macrophylla.* The luxuriant herbaceous layer includes many ferns which add to the appearance of mesophytism and a great variety of other plants as:

Adiantum pedatum
Aspidium noveboracense
Aspidium marginale
Asplenium angustum
Phegopteris hexagonoptera
Polystichum acrostichoides
Osmunda cinnamomea
Osmunda Claytoniana
Arisaema triphyllum
Smilax herbacea
Disporum lanuginosum
Disporum maculatum
Trillium grandiflorum
Medeola virginiana
Smilacina racemosa
Cypripedium parviflorum pubescens
Orchis spectabilis
Cimicifuga racemosa
Heuchera longiflora
Astilbe biternata
Podophyllum peltatum
Silene virginica
Anemonella thalictroides
Thalictrum dioicum
Geranium maculatum
Circaea luteliana
Aralia racemosa
Panax quinquefolia
Desmodium grandiflorum
Amphicarpa monoica
Vicia caroliniana
Viola rotundifolia
Viola blanda
Sanicula sp.
Asclepias quadrifolia
Asclepias phytolaccoides
Collinsonia canadensis
Eupatorium urticaefolium
Eupatorium purpureum
Prenanthes serpentaria
Aster divaricatus
Solidago caesia.

Nowhere else on the ascent of Pine Mountain has a community of this type been encountered. A broad trough 100 to 200 feet in depth, drained by streams, reduces the extreme insolation to which the southeast face of the mountain is subjected, and the topography is such as to permit soil accumulation. The underlying rock is nowhere exposed; it breaks down to form a clay soil, thus differing from all soils previously encountered. There is no line of demarcation between humus and mineral soil as has been evident in all areas except *6* and *9;* here as nowhere else on this slope a typical mull has developed. The upper five or six inches of soil is loose and crumby; at about six inches it becomes compact and clayey. In acidity as well as in structure, this soil differs from others: light humus or H-horizon, pH 6.69; crumby layer, pH 6.94; deeper clayey layer, pH 6.52.

The features here described are those encountered along the line of the profile. Up or down stream in the trough (a longitudinal valley) those features primarily related to depth of the trough vary. These are considered with the vegetation along a stream (see areas *R1* and *R2* of ravines of the dip slope).

17.—The final ascent to the mountain crest rises from this trough. The lower slopes share some of the features of the trough, though the most mesophytic species and those most typical of mull soon drop out, as the soil again becomes sandy and acid (pH 4.66 - pH 4.91). The forest at first is largely tulip, chestnut and chestnut oak, giving way up-slope to chestnut oak-chestnut;

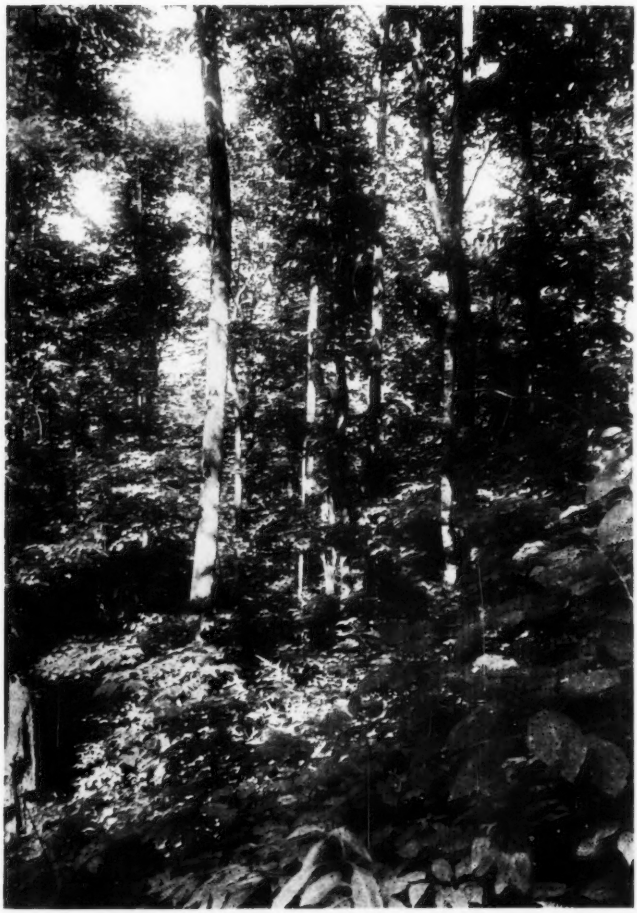

Fig. 13. Mixed mesophytic forest of upper trough, *f*. Within the range of the picture are tulip, cucumber, ash, red maple and chestnut trees. *Hydrangea arborescens* (right) and *Astilbe biternata* (center) in bloom.

chestnut oak is increasing in importance in the understory with the dying out of chestnut. Ericads again increase in importance and the herbaceous flora is poor. Upward the forest becomes more open, the chestnut oaks are lower and spreading (the typical rock ridge and slope form), pines enter, and heaths are more important. Duff development is evident and the soil is more acid (pH 4.23 - 4.83). In the low gaps which notch the mountain crest (indicated by dotted line of profile, Fig. 1) this forest or the oak-chestnut forest continues to the top. On the slopes of the higher knobs, the uppermost forest is an open pine forest (pines 60-80%) with an admixture of oaks and chestnut (Fig. 14). The composition of a representative example is:

pitch pine	43%	scarlet oak	6%
scrub pine	17	yellow pine	4
chestnut oak	17	sour gum	1
chestnut	12		

The ground layer in this light forest is continuous; grasses *(Andropogon scoparius* and *Sorghastrum nutans)* are important and shrubs more scattered than on the lower sandy soil slopes. In aspect the community is essentially savanna. Some of the herbaceous plants of the lower sandy slopes *(Lespedeza* spp., *Chrysopsis graminifolia, C. mariana, Aster linariifolius)* are scattered through the grass; *Aletris farinosa* is always abundant. The soil profile shows but a slight amount of surface litter; a shallow gray sandy-fibrous layer (pH 4.57) and deeper yellow sandy soil (pH 5.00).

B.—The Mountain Summit

At intervals along the summit of Pine Mountain (area *18)* the last sandstone stratum (stratigraphically the lowest) extends far up forming prominent

Fig. 14. The summit of Pine Mountain at High Rock (alt. 3200 ft.) showing jagged and broken edges of the upturned stratum which forms the mountain crest. Open pine forest of area *17* to right; northwest slope forest of area *19* to left. In the distance. the Cumberland Plateau about 1500 feet below.

projecting knobs jaggedly broken along the ridge crest (Figs. 14, 15). On the one side is the steep dip slope, on the other, high cliffs whose bases rise from the forest-clad mountain slope below. In places this narrow sandstone ridge supports gnarled or stunted trees. Generally it is open and shrubs are the conspicuous vegetation. Most interesting of these is *Rhododendron catawbiense* which in

Fig. 15. The scarp slope of the mountain crest at High Rock. *Rhododendron catawbiense* (right), *Kalmia*, *Vaccinium* and *Gaylussacia* grow from crevices on the cliff face. Nearest rock on right nearly covered with *Gyrophora*.

places forms a fringe along the cliff summit (Fig. 16). It grows in the most exposed, most extreme situations along the immediate crest and from crevices on the cliff face (Fig. 15). Other shrubs of the summit are *Rhododendron maximum* (always dwarfed in this situation), *Kalmia, Gaylussacia, Vaccinium stamineum, V. vacillans, V. corymbosum,* and occasionally *Robinia* sp. Away from the margin on the dip slope are patches of *Gaylussacia* and *Vaccinium vacillans,* and scattered herbaceous plants—*Andropogon scoparius, Danthonia sericea, Solidago odora, Chrysopsis graminifolia, Sericocarpus asteroides, Aster surculosus.* This slope is exposed to the most extreme insolation, usually facing south or southeast and is little protected by the open forest below. Crevices of the nortthwest-facing cliff of the scarp slope support, in addition to the heaths mentioned, stunted plants of chestnut oak, birch, Amelanchier and Clethra; patches of *Polypodium virginianum* in sheltered crannies; and clumps of *Campanula divaricata.* Insolation is not so extreme on this face, but exposure to wind is even more extreme, for there are *no* comparable heigths to the west.

C.—Ravines of the Dip Slope

Most of the longer and more important streams of the dip slope start in the uppermost trough, *f,* or receive lateral tributaries from this trough. From thence they descend by a course more or less transverse to the outcrop of strata. In general, five principal divisions (designated as *R1* to *R5)* are recognizable in such streams: (1) the upper longitudinal valley, (2) the upper transverse valley, (3) the gorge, (4) the lower valley, and (5) the mouth. No sharp limitations can be made between these divisions of a typical stream and all are not everywhere discernible. The vegetation will be considered in sequence from the headwaters downward.

R1.—A narrow wet flat broadening here and there into swampy patches borders the stream headwaters. *Sphagnum, Catharinea* and *Mnium* form thick cushions. The swamp herbaceous vegetation includes *Osmunda cinnamomea,* grasses and sedges *(Glyceria nervata, Scirpus atrovirens, Eleocharis* sp., *Carex* spp.), *Juncus effusus, Habenaria* sp., *Boehmeria cylindrica, Polygonum sagittatum, Apios tuberosa, Impatiens biflora, Oxypolis rigidior, Viola cucullata, Mimulus alatus, Chelone glabra, Phlox maculata, Lobelia cardinalis, Eupatorium maculatum, Solidago aspera, Aster prenanthoides* and *Senecio aureus.* In one such swamp area, *Orontium aquaticum* is an important species. Locally, the swamps are overgrown with thickets of red maple or of Rhododendron; in these, Sphagnum is almost the only ground cover with some *Viola blanda* and *Mitchella repens.* Drier and denser Rhododendron thickets, sometimes acres in extent, are without ground cover except occasional plants of *Cypripedium acaule* and *Listera Smallii.*

The forest of the slopes of these upper longitudinal valleys (see area *16)* varies in composition from place to place, the forest type usually bearing some relation to direction of valley or shelter. Because of the general N.E.-S.W.

Fig. 16. *Rhododendron catawbiense* on the summit of Pine Mountain at High Rock. Valleys in the Cumberland Plateau below are 2000 feet lower than the site of this bush.

trend of the trough, the streams flow in northerly or southerly directions; the valleys of the latter direction are slightly less mesophytic. Examples are:

a. Head of northeast flowing stream in upper trough:

tulip	54%	beech	3.5%
chestnut	34	red maple	1.5
chestnut oak	7		

b. Head of southeast flowing stream in upper trough:

chestnut oak	40%	scarlet oak	5%
chestnut	20	pitch pine	2.5
tulip	16	red maple	1+
sour gum	14	locust	1+

Red oak, white oak and hickory are sometimes present in small numbers. The understory in these forests includes the same species as the canopy and dogwood, Sassafras, sourwood and mountain magnolia. An open heath layer may or may not be present according to the depth of the valley and the nature of underlying rock.

R2.—The stream in this portion of its course is unrejuvenated; the downcutting following the uplift of the Cumberland peneplain not yet having deeply trenched the resistant and massive sandstone forming crests *V* and *VI*.

Near the outlet of a longitudinal tributary as it turns to join or become a transverse stream, the beginning of trenching is evident; the formation of a valley within a valley is reflected in the vegetation. The forest is hemlock, tulip, white oak and chestnut with occasional yellow birch and mountain magnolia. Rhododendron and Kalmia form dense thickets on the slopes, together with a few other shrubs, as *Pyrularia, Clethra, Acer pennsylvanicum, Evonymus americanus* and *Viburnum cassinoides*. The herbaceous vegetation becomes sparse, in contrast to that of the slopes of the trough, *f*, (area *16)*, and includes such extreme shade plants as *Aspidium noveboracense, Epipactis pubescens, Anemone quinquefolia, Chimaphila maculata* and *Viola rotundifolia*, which can grow in the now sandy soil or hemlock and Rhododendron duff. The higher slopes above the trenched valley begin to reflect the influence of slope exposure; northerly slopes retain the rich and varied mesophytic vegetation of the type already described for area *16* (Fig. 13); southerly slopes begin to show that character of all sandy soil areas of the dip slope of Pine Mountain.

R3.—The gradient of the stream increases greatly as it cuts through the massive strata which form crests *V* and *VI*. These sandstones now form high cliffs hemming in a valley whose slopes below the cliffs are steep talus accumulations (Fig. 17). The valley is now better described as a gorge. Regardless of direction, the forest is mesophytic, with a high percentage of hemlock. The forest of the slopes below the cliffs in a south-flowing stream (tributary to Bad Branch) is as follows:

hemlock	56%	birch	
tulip	11.6	chestnut oak	
yellow birch	9.6	red oak	
red maple	5.5	sour gum	10%
basswood	3.4	mountain magnolia	
beech	2.7	cucumber tree	
chestnut	2.7	hickory	

This is a forest of large trees, the hemlock 10 to 12 feet in circumference, B.H. In the understory are the same species and other smaller tree species and shrubs: *Oxydendrum arboreum, Magnolia tripetala, Ilex opaca, Rhododendron, Clethra, Hydrangea arborescens, Hamamelis, Viburnum acerifolium, Kalmia, Psedera quinquefolia* and *Rhus Toxicodendron*. The herbaceous growth is less luxuriant than in the higher mesophytic forest, reflecting the influence of an increased percentage of evergreens in the canopy. It includes *Polystichum acrostichoides, Asplenium angustum (A. filix-foemina), A. acrostichoides, Aspidium spinulosum, Adiantum pedatum, Lycopodium lucidulum. Arisaema quinatum, Medeola virginiana, Clintonia umbellulata, Asarum virginicum, Laportea canadensis, Tiarella cordifolia, Circaea lutetiana, Viola rotundifolia, V. hastata, V. rostrata, Meehania cordata, Mitchella repens, Eupatorium urticaefolium, Aster divaricatus*.

As the valley crosses successive layers of sandstone, it alternately narrows and widens slightly. Cliffs appear at intervals, sometimes low, sometimes high on the slope. As most of the streams cut somewhat obliquely to the dip

Fig. 17. High cliffs hem in valleys of the dip slope where they cross the massive sandstones (area *R3*). This south-facing cliff supports little vegetation. The dead trees are chestnut.

various overhangs and sloping ledges are formed. Where dipping strata form ledges some of the features of the "false summits" are repeated: lichen and moss mats and heath shrubs with occasional pines. On the shaded cliff faces, *Heuchera parviflora* var. *rugelii, Silene rotundifolia* and *Asplenium montanum* usually occur. On southerly cliff faces, ericaceous shrubs form lines along bedding and joint planes; otherwise these cliffs support little except lichens. Where cliffs or rock outcrops occur low on the slopes, hence near the stream in the deeper part of the valley, they are covered by deep mats of mesophytic mosses *(Thuidium* and *Mnium),* ferns *(Polypodium virginianum, Camptosorus rhizophyllus,* and sometimes *Aspidium marginale)* and *Mitchella repens* (Fig. 18). Longitudinal tributaries cutting deeply in lower troughs (as *c)* are of rare occurrence. A portion of Bad Branch is of this type and is mentioned because of the exceptional features of this portion of the valley. Hemlock is dominant, accompanied by yellow birch, tulip and mountain magnolia. Rhododendron and Kalmia, with scattered holly and Clethra, form almost impenetrable thickets. In the more open areas beneath the hemlocks, in the deep hemlock duff, is a characteristic herbaceous community made up of *Trillium undulatum, Chimaphila maculata, Epipactis pubescens, Mitchella repens, Medeola virginiana* and *Lycopodium lucidulum.* On the low sandstone cliffs here bordering the valley are great humps of *Sphagnum compactum* and on wet mossy ledges of the cliffs, *Saxifraga leucanthemifolia, Lycopodium lucidulum, Aspidium marginale* and *Cymophyllus (Carex) Fraseri.* There is no streamside vegetation as the stream is cutting in a resistant sandstone which here forms the floor of a high-level gorge, the outlet of which is a fall of sixty feet.

R4.—The gradient of the lower valley is considerably less than that of the gorge. The valley is deep and narrow but not, except locally, hemmed in by cliffs as above (Fig. 19). Hemlock, with a Rhododendron understory, is dominant near the stream, retaining an important place in the forest of the lower slope (Fig. 20). In one of the valleys opening directly to the *south*—a valley which in summer is the coolest and moistest observed, though in spring before leafing of the deciduous trees is complete, excessively hot—all boulders and rock ledges are deeply moss-covered to the water's edge, and a remarkable assemblage of northern and high mountain species, associated with other extreme mesophytes, is found including *Oxalis montana, Lycopodium lucidulum, Circaea alpina, Houstonia serpyllifolia, Cymophyllus (Carex) Fraseri, Boykinia aconitifolium, Viola blanda, V. cucullata* and *Thalictrum clavatum.* While not to be thought of as typical, the occurrence of such a community at the foot of the mountain (elevation 1800 feet) is worthy of note.

A short distance away from the stream, the hemlock-Rhododendron community gives way to a mixed forest (Fig. 19) of mesophytic species similar to

Fig. 18. Birch (near) and chestnut oak in gorge in which hemlock and Rhododendron are important. The cliff low in the gorge is covered with deep mats of moss, polypody, and walking ferns.

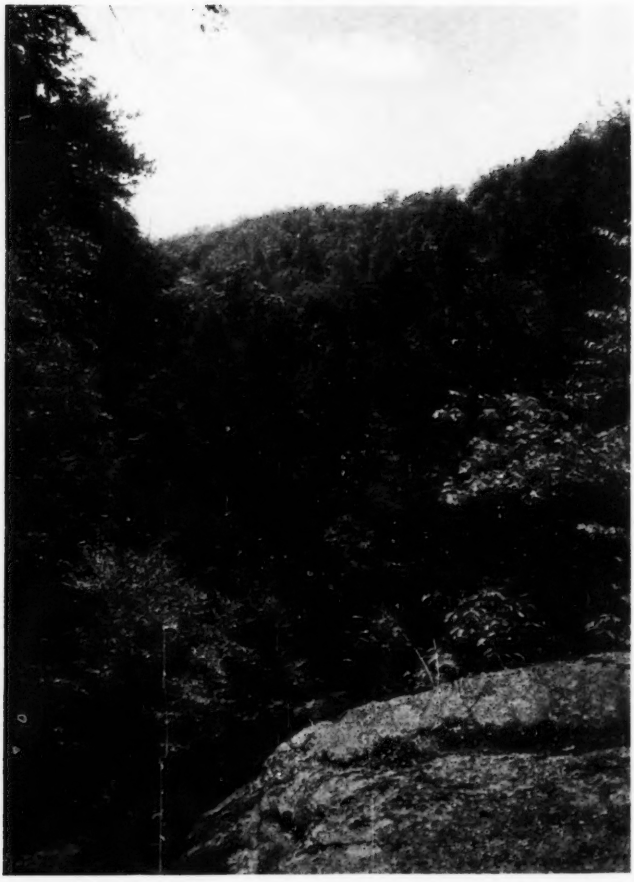

Fig. 19. Looking south down the lower valley of Bad Branch *(R4)*. The importance of hemlock in this forest is evident.

Fig. 20. Rhododendron forms the understory near the stream in the lower part of the valley *(R4)*.

that on the slopes of the gorge farther upstream:

hemlock	45%	chestnut oak	3
red maple	14	mountain magnolia, red oak, sourwood, sour gum, cucumber tree	8
white oak	13		
tulip	7		
yellow birch	6		
chestnut	4		

Beech may be persent in this mixed forest in sufficient numbers to be one of the five or six most important species; buckeye also is sometimes present. Away from the stream, Rhododendron soon becomes unimportant in the understory, its place is taken by Hamamelis, Pyrularia, Clethra, Evonymus and sometimes *Magnolia tripetala.* The ground layer is very open, made up of scattered plants of *Epigaea, Galax, Gaultheria, Mitchella, Viola rotundifolia, V. hastata, Medeola, Pogonia verticillata, Cypripedium acaule.* Where northerly slopes of the valley become clayey (as is frequently the case where the stream valley comes through area 2 of the profile) the forest changes to one in which sugar maple, beech and white oak are the most important species with red maple, chestnut and sour gum as minor constituents; dogwood, Carpinus and papaw *(Asimina triloba)* are important in the understory; the herbaceous layer contains a greater variety of species among which ferns and such plants as *Geranium maculatum, Tiarella cordifolia, Astilbe biternata, Cimicifuga racemosa, Amphicarpa monoica, Collinsonia canadensis* and *Eupatorium urticaefolium* are important. The remainder of the valley slopes are indistinguishable from the slopes of area *1* of the profile.

R5.—The lowest part of the stream course, usually less than one-fourth of a mile in length, where the valley opens up as it emerges from the mountain, is omitted from this discussion as these areas are always utilized for homes or farms and so little of the vegetation remains. The stream itself, no longer swift, is generally bordered by alders and river birch. Scattered trees of beech, white oak, chestnut, hemlock, red maple and basswood point to the former occupancy of stream flats by a mixed mesophytic forest.

D.—The Northwest Slope

The steep northwest slope of Pine Mountain (areas *19, 20, 21)* everywhere supports mixed mesophytic deciduous forest (Figs. 21, 22). The forest canopy is made up of some twenty-five species of which basswood, buckeye, sugar maple and tulip are most important and comprise about 65 per cent of the stand. Red oak, cucumber tree, ash and walnut are generally present though seldom numerous. On the lower slopes, beech is important; on the uppermost, chestnut.

A picture of the forest composition of the mid-slope (area *20)* can be

Fig. 21. The steep northwest slope of Pine Mountain. The dead trees in the foreground are chestnuts on the mountain summit.

Fig. 22. One thousand feet vertically of forest-clad mountain slope—the northwest side of Pine Mountain above Line Fork. The light spots are basswood trees in bloom. The summit cliffs and broken fringing forest of the mountain crest plainly visible. Photograph taken from lower summit of an adjacent ridge; pine in right foreground on this ridge.

gained from a composite list made up from five representative areas in which 273 trees were counted:

basswood	19.0%	cucumber tree	3.3
buckeye	18.0	walnut	3.0
sugar maple	14.3	ash	2.2
tulip	13.5	elm	2.0
red oak	8.4	chestnut oak	.8
chestnut	8.4	red maple	.4
hickory (3 spp)	6.0	sour gum	.4

In many places the large tulip trees have been cut out. Other species of the forest which did not occur in the areas counted are:

beech	black oak
white oak	locust
butternut	mulberry
hemlock	mountain magnolia

This forest type (Fig. 23) is one of the most important of the Cumberland Mountains between 2000 and 3000 feet, though at the higher elevations tulip drops out and sugar maple becomes relatively more important. It is there best designated as sugar maple-basswood-buckeye; still higher, yellow birch (or *Betula alleghaniensis)* takes the place of buckeye. This is a luxuriant forest of very large trees occupying slopes so steep that ascent or descent is in places almost impossible. The ground is rocky, chunks of sandstone or limestone or both, depending upon elevation on the slope, are everywhere. Between the rocks and covering them in many places is rich deep soil; the humus is thoroughly incorporated with the mineral soil forming mull. In pH values, the soils contrast with anything on the other side of the mountain, ranging near the surface from pH 7.28 on upper slopes to pH 7.87 in typical basswood-buckeye-sugar maple-tulip forest, and at six inch depth from pH 6.26 to pH 7.20.

The understory is composed of canopy species and in addition dogwood, redbud, striped maple (upper slopes), Sassafras, papaw, Carpinus and Ostrya. Shrubs and vines include *Benzoin aestivale, Hamamelis virginiana, Hydrangea arborescens, Cornus alternifolia, Sambucus canadensis, Viburnum acerifolium, Aristolochia macrophylla, Clematis virginiana, Psedera quinquefolia, Rhus Toxicodendron, Vitis cordifolia, Menispermum canadensis.* The herbaceous growth is more varied and luxuriant than encountered elsewhere,[9] approached

9 As no lists were made earlier than June, early maturing spring forms, as Dicentra, have probably been overlooked.

Fig. 23. Buckeye (11 feet in circumference B.H.) with sugar maple and basswood in forest of northwest slope of Pine Mountain. Papaw in the understory.

only by that of parts of the highest trough, *f*, area *16*. Included are:

Phegopteris hexagonoptera
Adiantum pedatum
Asplenium angustifolium
Asplenium acrostichoides
Asplenium angustum
(A. filix-foemina)
Aspidium Goldianum
Aspidium spinulosum
Camptosorus rhizophyllus (on rocks)
Polystichum acrostichoides
Botrychium virginianum
Arisaema triphyllum
Uvularia grandiflora
Smilacina racemosa
Disporum lanuginosum
Disporum maculatum
Polygonatum commutatum
Trillium grandiflorum
Trillium erectum
Dioscorea villosa
Laportea canadensis
Pilea pumila
Asarum canadense
Stellaria pubera
Ranunculus recurvatus
Ranunculus hispidus
Thalictrum dioicum
Anemonella thalictroides
Hepatica acutiloba
Anemone quinquefolia
Clematis viorna
Cimicifuga racemosa
Podophyllum peltatum
Caulophyllum thalictroides
Sanguinaria canadensis
Sedum ternatum
Astilbe biternata
Tiarella cordifolia
Aruncus sylvester
Geum canadense
Amphicarpa monoica
Geranium maculatum
Impatiens pallida
Hybanthus concolor
Viola canadensis
Viola papilionacea
Circaea lutetiana
Panax quinquefolia
Aralia racemosa
Sanicula sp.
Osmorhiza Claytoni
Osmorhiza longistylis
Cryptotaenia canadensis
Phlox divaricata
Hydrophyllum canadense
Hydrophyllum virginianum
Phacelia bipinnatifida
Cynoglossum virginianum
Collinsonia canadensis
Monarda fistulosa
Stachys cordata
Galium spp.
Eupatorium urticaefolium
Solidago caesia
Solidago latifolia
Aster cordifolius
Aster divaricatus
Polymnia canadensis

The forest of the mid-slope varies but slightly from place to place. On convex portions of the slope, chestnut and cucumber become somewhat more important, basswood less important, and buckeye drops out:

chestnut	38%	red oak	5
tulip	14	walnut	5
Sugar maple	10	chestnut oak	4
cucumber tree	10	sour gum	4
basswood	10		

The undergrowth here is poorer, many of the most mesophytic species being absent.

Where the "Big Lime" formation (a Mississippian limestone) forms ledges or low cliffs *(VII* on profile, Fig. 1) the forest may be locally interrupted by a more xeric community. Ostrya and redbud skirt the upper edge of the cliff, usually accompanied by *Celastrus scandens* and *Rubus odoratus*. Rock surfaces support *Pellaea atropurpurea* and *Camptosorus rhizophyllus;* the herbaceous community of crevices and shallow soil accumulations includes

Hystrix patula, Thalictrum dioicum, Polygala Senega, Euphorbia corollata, Taenidia integerrima, Solidago ulmifolia and *Brachychaeta sphacelata.* This variation is obviously related to soil and soil moisture.

Other variations in the forest of the northwest slope occur which appear to be in part altitudinal, in part due to soil influence, and in part to exposure.

The uppermost slopes of the mountain, the slopes immediately under the summit cliffs (area *19),* are even steeper than those below, formed to some extent of talus from the summit sandstone. The forest continues of about the same composition as on the mid-slope; wild cherry is present, chestnut and cucumber tree are somewhat more abundant and Oxydendrum is in the understory. Due largely to a poorer herbaceous layer, this forest loses something of the decidedly mesophytic aspect of the mid-slope. *Dicksonia punctilobula* and *Aspidium noveboracense* take the place of the Adiantum and Aspleniums below. Here are *Clintonia umbellulata, Disporum lanuginosum, Heuchera longiflora, Aruncus sylvester, Geranium maculatum, Asclepias phytolaccoides, Eupatorium purpureum* and *Steironema intermedium. Clethra acuminata* grows in sheltered places at the foot of cliffs. Where not covered by talus, low cliffs of evenly bedded flagstone and shale on the highest slopes support *Polypodium virginianum, Aspidium marginale, Camptosorus, Adiantum, Heuchera* sp., *Sedum ternatum, Campanula divaricata* and *Aster divaricatus.*

Beech, while always important in the forest of the lowest slopes of the mountain everywhere drops out between 2000 and 2200 feet, sometimes lower, and for this reason is not a common component of the mid-slope forest (area *20).* This altitudinal response is apparent not alone on Pine Mountain but on Black Mountain as well; it is entirely independent of shelter. The presence or absence of beech cannot be used as an indication of degree of mesophytism.

The lower slope forest (area *21)* is a mixed mesophytic forest in which beech is co-dominant with sugar maple, tulip, buckeye and basswood or assumes an even more important place, forming sometimes nearly fifty per cent of the stand. White oak is usually a constituent of this forest. In undergrowth this forest is scarcely distinguishable from the mid-slope forest; *Disporum maculatum* is not present; *Phlox divaricata* is more important; *Meehania cordata* and *Bignonia capreolata,* not present above, are added.

Another variant of the lower slope forest in which beech is important is found on projecting sandstone slumps and ridges. Here beech is associated with hemlock, chestnut and chestnut oak. Some *Vaccinium vacillans* and *Kalmia* occur in the understory and the herbaceous growth is relatively poor. The humus layer in these areas is duff-like; the soil sandy pale grayish with mycelia above (pH 6.35) and sandy gray at six inches (pH 5.50). In soil and forest aspect these limited areas resemble parts of the other slope of the mountain more than they do adjacent communities.

The forest of the northwest slope merges with that of the valley at its base. The most conspicuous difference, where a valley flat is present (area

22) is noted in the incerase in beech to a place of dominance above all other mesophytic species (Fig. 24):

beech	62%	mountain magnolia	7
basswood	7	ash	3
hemlock	7	red oak	3
red maple	7	sour gum	3

The understory is of the same species, together with dogwood, Carpinus, papaw, and locally, Rhododendron. This type of forest (with minor variations) is found rather generally in comparable situations throughout the Cumberland Mountains and Cumberland Plateau; it, however, is seldom represented by more than the merest fragments. The forest of the lowest division of ravines *(R5)* of the southeast slope of Pine Mountain may have been of this type in places.

The northwest or scarp slope of Pine Mountain has been shown to be essentially uniform throughout, to lack the diversity and contrasts which mark the southeast or dip slope. The relation between vegetation and rock outcrop, so evident on that slope, is almost absent here. As streams are unimportant, scarcely indenting the slope except in rare instances, there is no appreciable change in vegetation near streams.

That the presence or importance of beech low on the northwest slope (area *21)* and on the stream flat (area *22)* shall not be interpreted as related primarily to slope exposure and mesophytism, the adjacent forest of southeast slopes facing Pine Mountain should be considered. It will be recalled that the lowest slopes of the southeast face of Pine Mountain (area *1)* are, in general, white oak-beech, though nowhere was the forest in such condition that composition could be determined. Here, again, is a similar forest (area *23),* in which beech and white oak are co-dominant in a mixed forest:

beech	27%	butternut	2
white oak	22	bitternut hickory	1
hemlock	15	sourwood	1
sugar maple	9	birch, cucumber tree, chestnut, buckeye, mountain magnolia	4
red maple	8		
red oak	4		
tulip	4		
sour gum	3		

The undestory contains in addition, dogwood, redbud, service berry, umbrella magnolia, holly, and papaw. Shrubs and woody vines include *Benzoin aestivale, Hamamelis virginiana, Evonymus americanus, Psedera quinquefolia, Rhus Toxicodendron, Rhododendron maximum* and *Bignonia capreolata.* The herbaceous vegetation is neither as rich nor as varied as that of the middle

Fig. 24. The beech forest of the valley flat, area *22*.

and lower mountain slope, but recalls that of the higher slopes of the northwest side of the mountain. Here are:

Aspidium noveboracense
Aspidium spinulosum
Aspidium marginale
Asplenium platyneuron
Phegopteris hexagonoptera
Botrychium virginianum
Arisaema triphyllum
Medeola virginiana
Uvularia perfoliata
Aristolochia serpentaria
Laportea canadensis
Cimicifuga racemosa
Tiarella cordifolia
Geranium maculatum
Oxalis violacea
Viola blanda
Viola rostrata
Viola hastata
Chimaphila maculata
Phacelia bipinnatifida
Mitchella repens

In this area the influence of underlying sandstone is reflected to a slight extent. The composition of this forest—a type rather general on the lower mountains adjacent to Pine Mountain, and even on certain projecting ridges which may properly be considered a part of the northwest slope of Pine Mountain—varies from place to place in the relative importance of white oak and beech, and in the number and importance of constituent species:

white oak	48%	sugar maple	4
hemlock	18	red oak	2
beech	11	bitternut hickory	2
tulip	6	sour gum	2
birch	5	chestnut	2

Higher on slopes, white oak may comprise as much as sixty per cent of the stand:

white oak	60%	black oak	4
beech	15	bitternut hickory	3
chestnut	9	red maple	2
tulip	5	sour gum	2

It may readily be seen from this, that a number of the mesophytic tree species, particularly sugar maple, will drop out sooner than beech with decreasing mesophytism or increasing acidity, and that beech is an important constituent of other than the most mesophytic forests.

IV.—Discussion

The plant communities of Pine Mountain have been described in detail, the specific features and contrasts noted, (1) because of the striking dependence of communities on local factors and the relation of these to geological structure, (2) because of the opportunity afforded to consider community range or fidelity of tree species, (3) because of the presence of a few species in certain communities best explained on a basis of physiographic history, and (4) because of the significance of the communities here displayed in connection with the problem of deciduous forest climaxes.

COMMUNITY RANGE AND IMPORTANCE OF TREE SPECIES

FOREST TYPES		AREA NOS.		TREES	Pitch pine, Pinus rigida	Yellow pine, Pinus echinata	Scrub pine, Pinus virginiana	Chestnut oak, Quercus montana	Chestnut, Castanea dentata	Scarlet oak, Quercus coccinea	* Mountain magnolia, Magnolia Fraseri	Tulip tree, Liriodendron tulipifera	* Sassafras, Sassafras variifolium	* Service berry, Amelanchier canadensis	Red maple, Acer rubrum	Sour gum, Nyssa sylvatica	* Sourwood, Oxydendrum arboreum	* Persimmon, Diospyros virginiana	Pignut hickory, Carya glabra	White-heart hickory, Carya alba
Pine-oak	Pine	5, 10, 14, 17	SOUTHEAST SLOPE		X	X	X	X	x	x	x		x	x	x	x	x	x		
	Chestnut oak-pine	8, 14, 17			X		X	X	X	x	x		x	x	x	x	x			
Chestnut oak-chestnut	Chestnut oak	4a, 7			x	x		X	X	x		x	x	x	x	x	x			
	Chestnut-ch.oak-red maple-pine	4, 4b 17			X	X		X	X	x		x			X	x			x	
Chestnut-chestnut oak-white oak-tulip	Chestnut-white oak	2; 4c			x	x		X	X	x		x			x	x	x			
	Chestnut-wh.oak-tulip	9						x	X			X			x	x	x			
	Ch.oak-chestnut-wh.oak	10			x			X	X			x				x	x			
	Ch.oak-chestnut-tulip	6, R1b, 19			x			X	X	x	x	X	x		x	x	x			x
	Chestnut-tulip+···	1, 16 R1a						x	X		x	X			x	x			x	
Mixed Mesophytic	White oak-beech or White oak	1, 23	N.W. BASE						X			x		x	x	x	x			
	Beech-white oak+	23							x		x	x		x	x	x	x			
	Beech+·	22							x		x				x	x				
	S.maple-beech-wh.oak	1, 21, R4	N.W. SLOPE					x	x			X			x	x				x
	Basswood-s.maple-tulip-chestnut	19							X		x	X				x	x			
	Basswood-buckeye s.maple-tulip	20						x	x		x	X	x		x	x			x	x
	Hemlock+···	R1, R2, R3	RAVINE					x	x		x	X			X	x	x			

* indicates species of small stature wh

×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	Sour gum, Nyssa sylvatica
×		×			×	×		×	×	×	×		×	×	×	Sourwood, Oxydendrum arboreum *
															×	Persimmon, Diospyros virginiana *
	×						×					×				Pignut hickory, Carya glabra
	×		×					×								White-heart hickory, Carya alba
	×		×			×					×	×	×		×	Black oak, Quercus velutina
×	×	×	×	×	×	×	×	×			×					Red oak, Quercus borealis maxima
×	×	×	×		×	×		×	×	×	×	×	×			White oak, Quercus alba
×	×						×			×						Striped maple, Acer pennsylvanicum*
×	×		×	×	×	×	×	×		×			×			Dogwood, Cornus florida *
	×	×	×				×									Walnut, Juglans nigra
×					×	×	×							×		Birch, Betula alleghaniensis
×	×		×					×								Hickory, Carya sp.
×	×	×	×		×	×	×									Cucumber tree, Magnolia acuminata
		×														Wild cherry, Prunus serotina
	×						×	×								Black locust, Robinia Pseudo-Acacia
×	×		×	×	×	×	×									Beech, Fagus grandifolia
×	×	×	×		×	×										Sugar maple, Acer saccharum * A. nigrum
	×	×	×		×											Buckeye, Aesculus octandra
×	×	×	×	×			×									Basswood, Tilia heterophylla
	×				×											Butternut, Juglans cinerea
	×															Shell-bark hickory, Carya ovata
					×	×										Bitternut hickory, Carya cordiformis
	×		×													Ostrya, Ostrya virginiana *
×	×		×	×												Carpinus, Carpinus caroliniana*
	×		×													Elm, Ulmus americana

// stature which are usually confined to the understory. †Only along

		×				×											Butternut, Juglans cinerea
		×															Shell-bark hickory, Carya ovata
						×	×										Bitternut hickory, Carya cordiformis
		×		×													Ostrya, Ostrya virginiana *
	×	×		×	×												Carpinus, Carpinus caroliniana *
		×		×													Elm, Ulmus americana
		×					×										Mulberry, Morus rubra
	×	×		×	×	×	×										Papaw, Asimina triloba *
		×				×	×										Redbud, Cercis canadensis *
		×		×	×												Ash, Fraxinus americana & F. biltmoreana
	×	×		×	×	×	×	×				×					Hemlock, Tsuga canadensis
	×																Yellow birch, Betula lutea
	×					×											Umbrella tree, Magnolia tripetala *
	×					×											Holly, Ilex opaca *
																	River birch, Betula nigra †

*Only along streams in Rs. †Only along streams in Rs.

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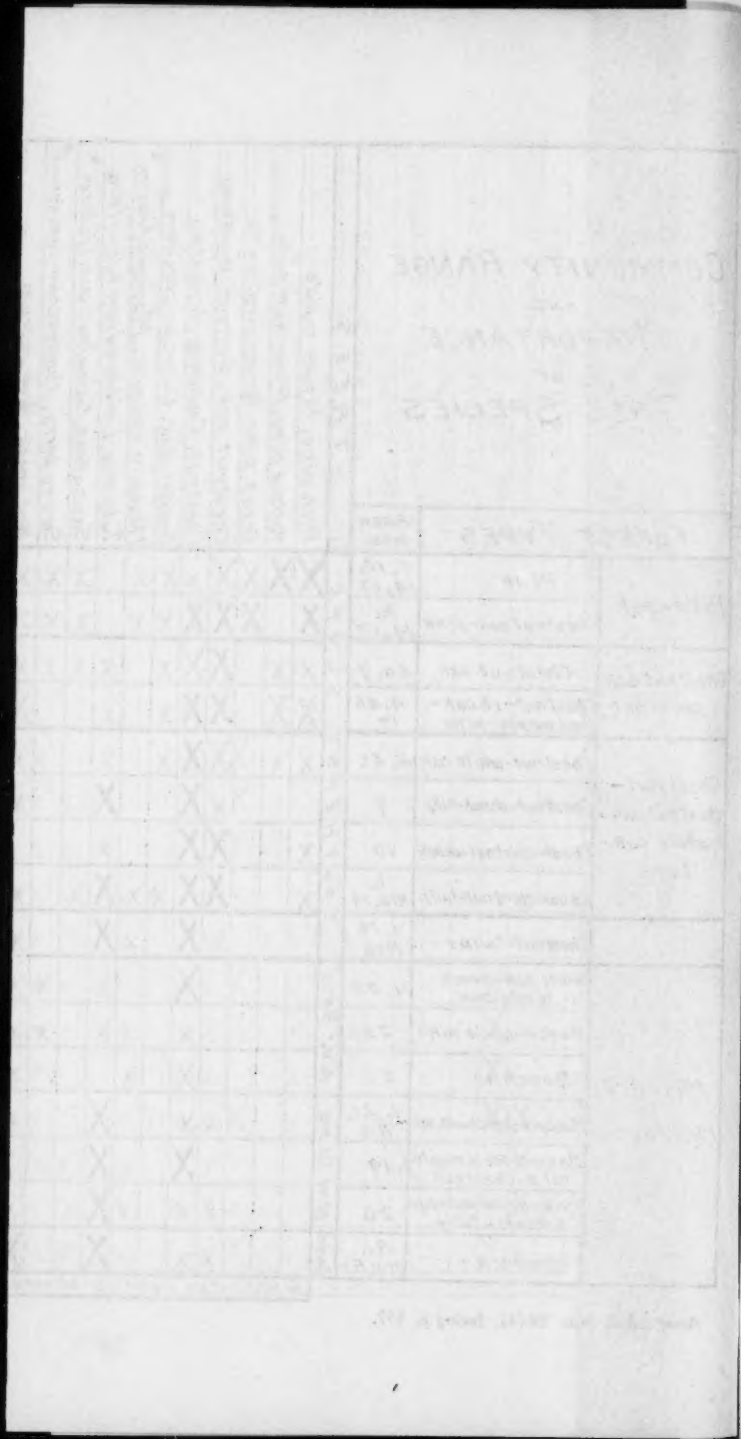

Within a limited area on this mountain are more different communities, more contrasts between communities, than in all the rest of the Cumberland Mountains. Due to topographic and soil influences combined very unlike plant communities exist side by side. The effect of "local climates" in determining forest types may be questioned for even "local climates" can scarcely be conceived of as changing radically in sixty feet—the limits within which pronounced changes in forest have been shown to take place (areas *5-6; 8-9; 14-15-16).* The prevailing mesophytic deciduous forest of the Cumberlands, though complex in segregation and grouping of its tree species, maintains its general character almost throughout.[10] Only here is there any real interruption. The effect of Pine Mountain is, then, to interpose in a region of climax forest communities of the mixed mesophytic climax, stripes and patches of unlike forest.

The forests of Pine Mountain contain thirty-four canopy species of which sixteen species attain an important position in one or more of the forest types and eleven tree species of lesser size which may be important in the under story (see Table). By a comparison of the composition of the communities, it may readily be seen that there is great difference in the community range or fidelity of the various species; some, as chestnut, occur in nearly every type; others, as sugar maple, are very limited. Fidelity and constancy of species are characters of importance in interpreting fragmentary communities. Due to the limited number of patches of each community studied, neither can be stated with accuracy according to a numerical scale (as defined by Braun-Blanquet, 1932). Yet an arrangement of forest types and tree species, as in the accompanying table, shows some very definite facts concerning significance of various species. The forest types are listed on a basis of increasing mesophytism. Dominants are indicated by **X,** important species by X, and all others by x. The selection of the symbol shown was determined in part from the composition lists given and in part from additional field notes.

It may be seen that the dominants of the most xeric communities are absent from or very unimportant in the mixed mesophytic forest communities; that most of the dominants of the mixed mesophytic forest are absent from the more xeric communities. The features of constancy and fidelity displayed here cannot of course be transferred to other geographic areas without careful checking, but within limits, they may be used in determining the spacial relations and extent of communities badly decimated by lumbering.

Obviously, the mere presence of chestnut means nothing, for it was found in every community studied; however, there are form differences between chestnut in mesophytic and xerophytic communities. Chestnut oak would appear to have little more significance, except that there is great difference in the form assumed in different communities (see Figs. 3 and 9). Tulip tree, too, has a wide community range, though generally most important in the more mesophytic forests. White oak may be associated with the most meso-

10 This generalization is based upon studies of forest types in progress in the Cumberland Mountains and Cumberland Plateau.

phytic species, as sugar maple, basswood and buckeye, be co-dominant with beech, or be associated with the more xeric chestnut oak or even pine.

The status of beech is of considerable interest. On Pine Mountain it has been shown that beech is altitudinally limited (as it is also on adjacent mountains, though it reappears there at close to 4000 feet); hence it is excluded from all except the communities of lower slopes. Below 2000 feet, and in the Cumberland Plateau generally, it is frequently associated with sugar maple, basswood, buckeye and tulip. Higher, where-beech is not important, the increased dominance of these species gives rise to one of the most important forest types of the Cumberland Mountains. The association of beech with white oak, or with white oak and chestnut (area *23)* or occasionally (as locally in area *21)* with chestnut and chestnut oak, forests in which sugar maple, basswood and buckeye are absent or unimportant, points to a wide range of habitat conditions suitable for beech. In these forests of white oak and beech the herbaceous vegetation is much less luxuriant and poorer in species than in other of the mixed mesophytic communities. The presence of beech, however indicative in some regions it may be of the most mesophytic conditions, is not here to be so interpreted.

Buckeye, basswood and sugar maple are more restricted, and it is the forest in which these three are important that the greatest number of tree species—thirty-two—occurs. Hemlock, while important only in ravine forests, is nevertheless erratic in its occurrence. Trees of lesser importance display comparable features as to community range. Sour gum may be present in any community. Mountain magnolia is either in the driest habitats, as cliff margins, or in the most mesophytic habitats; it is infrequent in intermediate habitats. Scarlet oak is strictly limited to the more xeric communities while red oak generally is more mesophytic. Dogwood occurs through a wide range of communities, sometimes becoming very important in the lower layer of oak or oak-chestnut forests. It becomes obvious that individual species in cut-over areas can, with few exceptions, not be considered as indicative of the former occupancy of certain types. Only by a careful consideration of combinations of species or of key species can a picture of the original distribution of the many segregates of the deciduous forest be reconstructed.

The community range and fidelity of herbaceous species appears to be in some instances even more marked than that of tree species. By a comparison of lists in the various areas, significant species may be selected.

The large number of forest communities distinguished—sixteen in the second column of the table—raises a question as to the status of each. In the older terminology, any one might have been considered an association, for each is relatively stable. It is possible, however, to group these, for a number of communities have one or even two dominants in common, though differing as regards other constituents. Such grouping is indicated in the first column, in which only four types are listed; the second and third of these might together perhaps be designated as oak-chestnut. All would then be referable to oak-pine, oak-chestnut, and mixed mesophytic types, each of which

may probably correctly be termed an association; in places, the pine-oak is doubtless an associes. Yet between these there is so much intergrading that distinctions are not clear cut. Apparently, each recognizable community is a segregate of a more complex one—an "association-segregate." The impossibility of holding to the three-association idea for the deciduous forest (Weaver and Clements, 1929, pp. 423, 453; Clements, 1934) is obvious, even from a study of such a limited area as this portion of Pine Mountain. There is here no "oak-hickory" and no "maple-beech," two of the so-called three associations of the deciduous forest climax. Hickory is not important in any community. Beech and maple together form an important part of only one of the seven communities of the mixed mesophytic forest; only the "oak-chestnut association" is represented. The relationships of the communities and a plan for their classification cannot be satisfactorily demonstrated without consideration of a much larger area.

The analysis of deciduous forest climaxes is the aim of field studies embracing a territory of which this is but a fractional part. Here it is desired to call attention to the very evident differences between and overlapping of the oak-chestnut segregates and the mixed mesophytic segregates, and particularly to the complexity of the mixed mesophytic forest. It is the mixed mesophytic forest in which the number of tree species reaches a maximum, not in the oak-chestnut forest as stated by Weaver and Clements (1929, p. 455), and in consequence it is this association which displays the greatest variations in composition. The importance of the mixed mesophytic association of the deciduous forest cannot be over-estimated. An understanding of it is essential to the understanding of deciduous forest. The complex mixed deciduous forest represents the great undifferentiated climax from which other simpler climax "associations" have been derived under stress of climatic change or migrating population. This will be demonstrated in a later paper. For further exposition of the principle, see "The undifferentiated deciduous forest climax and the association-segregate" (Braun, 1935).

The mosaic of communities on Pine Mountain at first appears unorderly. There is no apparent sequence (excepting those pioneer communities of the sloping rock exposures), no constant inter-relation between communities. Changes are abrupt—within a few feet—or gradual. Yet communities of the same composition, the same specific content, recur again and again on the mountain. The regularity of appearance, the constancy displayed by separated patches of the same community, the frequent lack of sequence, suggest causal factors not residing in the vegetation, for the reactions brought about by vegetation are orderly in their sequence and result in orderly development of vegetation. Here the vegetation reflects edaphic influences strong enough, extreme enough, to overcome this orderly sequence, to interrupt or to modify the effects of the regional factors.

While some of the communities are conceivably developmental stages—though no actual indication of progress is evident except in pioneer lichen, moss and shrub stages of the sloping sandstone exposures of the various crests

—each is relatively permanent, reproducing itself, as can be seen by comparing canopy and understory. A certain permanence and stability has been reached, an equilibrium between vegetation and environment. The nice adjustment between community composition and slope exposure, displayed again and again, suggests in these instances a controlling influence of this local factor. While some of the variations in communities are definitely related to slope exposure, the contrasts displayed are greater than on other nearby mountains. The vegetation of the southeast face of Pine Mountain is as a whole much more xerophytic than is that of equally steep or even steeper southwest slopes of adjacent Black Mountain. In the case of Pine Mountain, slope exposure is due to geological structure which in turn results in shallow soil in many parts of the southeast face. Coupled with this is the nature of the rock which yields on weathering a non-calcareous sandy soil. Possible depth of soil accumulation is affected by the dip of strata. The upper slopes of strata, dipping at about 30°, are most unsuitable for accumulation of weathered material and humus. Thus these areas are constantly kept in pioneer condition. The reactions of the type of woody vegetation which first comes to occupy such areas—heaths and pines—tend to modify the soil. This, combined with sunny exposure, coarse texture and the originally sandy condition favors the development of duff which in turn tends to exclude plants more characteristic of the regional forests.

The combination of edaphic factors here displayed—slope exposure, sandy soil, duff—together with the resultant types of forest, increases the fire hazard in spring when temperatures are high, exposure to sun extreme, and (again because of soil and type of forest) herbaceous vegetation at a minimum. Hence fire, as a factor affecting the development of vegetation, is more important than in adjacent habitats.

The intercalation of occasional shaley members between the sandstones in this part of the Pottsville series has resulted in certain erosion features favoring soil accumulation and in places higher moisture content. In such areas soil development has proceeded farther; soils are more nearly of the climatic type. Coupled with such soil differences which are dependent on geological structure and nature of material, are the topographic features which also result and which introduce slope contrasts.

The dip of strata tends to drain ground water down the southeast face, to rapidly carry water away from ridge crests, to feed permanent streams in the dip slope ravines. It also lessens the possibility of streams on the northwest face of the mountain and hence is in part indirectly responsible for the greater uniformity of that slope. If it were possible for a mountain with horizontal strata (instead of steeply dipping strata as here) to have the same form, and same steepness and direction of slopes, the local features would be different.

Such abrupt contrasts in vegetation as occur midway on the scarp slope of the deeper trough, *f*, (see areas *15, 16)* cannot be related to slope exposure for it does not change. Underlying rock and the soil derived from it change;

here a soil factor appears to control. On mature soils—those showing by their structure little or no relation to parent material (Wolfanger, 1930)—such abrupt vegetational changes are impossible in the absence of other controlling factors. We are confronted then with the necessity of recognizing here immature soils. Future development of these soils is conceivable and with that further development of vegetation. Only in parts of the upper trough, *f*, in ravines and on the northwest slope of the mountain and adjacent lower slopes are the soils of such character that they can be thought of as mature. Only there, then, has the development of vegetation progressed as far as is possible on mature soils of the climatic area under consideration. The development of vegetation over almost the entire southeast slope of the mountain must be thought of as held in check by immaturity of soil development. None, then, is of a type which can be considered as climax in the regional sense. Yet all (again excepting certain pioneer communities noted above) have reached a certain stability. Either we must consider each distinct stable community as subclimax to the theoretical climax which some day should occupy Pine Mountain (when and if local factors moderate in intensity) or we must consider each as an edaphic or physiographic climax.[11] Whichever interpretation is followed we are faced by the necessity of relegating each and every one of these stable communities of immature soils to a rank subordinate to the regional climax. A survey of the areas shows that all shrub, pine, pine-oak, oak, and oak-chestnut communities, with or without heath understories, occupy immature soils, soils in which the influence of parent material (here underlying sandstone) is evident. It shows also, that in every community in which there is a fair admixture of those tree, shrub and herb species generally thought of as the more mesophytic species, or of those generally thought of as indicative of mull (Romell and Heiberg, 1931; Lutz, 1932), the soil profile is that of more mature soils. It shows, furthermore, that in those areas of most mature soils the most complex forest communities (as to specific content) develop, forest communities which generally include several of the more typical members of the mixed mesophytic association of the deciduous forest, and in which the species characterizing (by dominance) the communities of the most immature soils are, except chestnut, unimportant or absent (see Table). Included in this last group are the forests of areas *16* (in part), *19, 20, 21* (except certain beech areas), *22, 23* (in part) and of most of the ravines. It may readily be seen that these forest communities are alike in certain features: large number of species; importance of such mesophytic species as maple, tulip, basswood, buckeye; absence of or unimportance of heath shrubs (except *Rhododendron maximum* and locally, red Azalea); and luxuriance of herbaceous layer. All may be thought of as mixed mesophytic deciduous forest. It is the *mixed mesophytic association* which should properly be considered the *regional climax*. It is represented here by a number of association-segregates (Braun, 1935).

In the ravines, the co-dominance of hemlock with the deciduous species in-

[11] Subclimax is used here as defined by Clements (1928, p. 107); physiographic climax as defined by Nichols (1923, p. 172). Subclimax as here used is the "proclimax" of Clements (1934).

troduces a question as to the propriety of considering these forests as equivalents of those without hemlock, *i.e.*, of considering the ravine forest as climax also. The interpretation of such forests as postclimax has been advocated (Clements, 1934). This view is at first sight supported by the fact that this is a ravine type; it is to be remembered, however, that the ravines of Pine Mountain in which hemlock is important are those formed by south- or southeast-flowing streams, that they are therefore open to the south; that hemlock is not confined to the gorges or lowest slopes, but enters the ravine forests near the headwaters. Because of the essential similarity in canopy composition (except for the hemlock), the similarity of understory,[12] and maturity of soils, it seems best to consider this ravine forest as a possible variant of the mixed mesophytic climax. The arbitrary exclusion of this from a deciduous forest climax because of the presence of a different growth form—evergreen tree—is not supported by the facts of composition, soil and occurrence. An exception should be made of such areas dominated by hemlock as were noted in upper Bad Branch *(R3)*. While there is an admixture of mesophytic deciduous species, these are not co-dominant; neither are the accompanying species (except tulip) important in the regional climax. To consider this community as a consociation of the mixed forest is not justifiable, for there are few features in common between this and the mixed mesophytic forests of ravines, other than that both contain hemlock. Here the reactions brought about by hemlock in a high-level sandstone valley have so modified the ground environment as to exclude most of the species of the mixed mesophytic forest. There is nothing to indicate that this community is a later development of the mixed mesophytic forest containing hemlock, nothing to justify its interpretation as postclimax for it does not occupy an unusually moist and sheltered ravine. In the absence of evidence it cannot be interpreted as a retrogressive stage (if the idea of retrogression be admitted). Rather it seems to represent an end stage in a possible exceptional development, or in an earlier clisere. The possible relic nature of the community is suggested by the presence here, and in the same valley farther downstream, of a number of high mountain and northern species.[13] The long course of physiographic history involving more or less complete cycles of erosion, the development of the Cumberland peneplain, its uplift and dissection and the climatic oscillations of the later Tertiary and Quaternary periods have been insufficient to remove, from the area now called Pine Mountain, all trace of mid-Tertiary vegetation. This is attested by certain species of limited geographic distribution: by *Rhododendron catawbiense* on the higher knobs of the mountain summit—knobs which were monadnocks on the Cumberland peneplain[14]; by the Coastal Plain species, *Orontium aquaticum,* in an unrejuvenated portion of a stream occupying the upper trough, *f*,—formerly a valley of the peneplain; by the group of typically high

12 The fact that the same understory may occur under different canopies or different understories under the same canopy, is recognized. (See also Cain, 1934.) Similarity of all layers, as here, emphasizes similarity of the complete layered community.

13 This problem of floristic affinities will be considered in a later paper: "Some relationships of the flora of the Cumberland Plateau and Cumberland Mountains in Kentucky."

mountain or northern species, as *Saxifraga leucanthemifolia, Oxalis montana,* and *Circaea alpina,* which here as in the Southern Appalachians, occupy areas in which some diversity of topography prevailed even at the time of maximum development of the peneplain. The presence of such diverse floristic elements and their age must be considered in postulating any far-reaching migratory swings, either north and south or east and west. These features are mentioned here because of the evidence they bring together of the possibility of long persistence of communities not climax in the regional and truer sense.

That much of the vegetation of Pine Mountain is in a state of arrested development, kept so by the influence of edaphic factors—slope and soil together with structure—is a strong argument for the effectiveness of these factors. The arrangement of the communities in developmental series is impossible; each is an ultimate stage, theoretically temporary but actually relatively permanent. Here, then, are a number of subclimax communities or physiographic climaxes, as well as a number of segregates of the mixed mesophytic association, the climatic climax. The recognition of the pine, pine-oak, oak and oak-chestnut communities as subclimaxes or physiographic climaxes in the geographic and climatic area concerned is important in the interpretation of the regional or true climax.

V.—Summary

The distribution of forest communities on Pine Mountain, in the Cumberland Mountains of southeastern Kentucky, is in the main controlled by slope exposure and soil. These are determined by geological structure; the mountain is a monoclinal ridge of strongly dipping strata.

The plant communities are treated in sequence along the line of a profile crossing the mountain and along a stream. These are considered in four groups: communities of (A) the southeast or dip slope, (B) the summit, (C) ravines of the dip slope, and (D) the northwest slope. The communities are shown to differ greatly from one another within short distances. Details of forest composition and soil are included as a basis for the discussion.

There is shown to be a striking dependence of communities on local factors which are in turn related to geological structure.

The community range of forty-five tree species is shown in a table, and the significance of certain species emphasized.

Sixteen forest types are considered which are treated as segregates of more complex communities, of which there are four. The mixed mesophytic forest association is considered the most important community of the deciduous forest—the regional climax today and the remnant of an undifferentiated climax from which other simpler climaxes have come.

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14 For certain data on the physiography of this section, the writer is indebted to Dr. N. M. Fenneman for the privilege of reading a portion of the manuscript of his book, "Physiography of the Eastern United States."

The permanent or relatively permanent character of all the forest communities is interpreted as evidence of the climax or subclimax nature of each. The relation of each to soils is considered.

Immature soils support subclimax communities or physiographic climaxes. Mature soils support the regional or true climax communities. All pine, pine-oak, oak and oak-chestnut communities are considered to be subclimax; the mixed mesophytic forest communities (association-segregates) are the true climax communities. These show considerable range in composition and constituent species; sugar maple, basswood and buckeye are the most important indicator species. The admixture of hemlock in a mixed forest does not remove it from the category of a segregate of the mixed mesophytic association.

The possible relic nature of one exceptional hemlock forest in which is an unusual group of herbaceous plants, is considered.

The recognition of the status of each community is essential to an understanding of deciduous forest climaxes.

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ECOLOGICAL STUDIES OF THE VEGETATION OF THE GREAT SMOKY MOUNTAINS

II. THE QUADRAT METHOD APPLIED TO SAMPLING SPRUCE AND FIR FOREST TYPES[1]

STANLEY A. CAIN

The purpose of this study is to examine the possibility of reducing the sampling of a forest community to the minimum consistent with the adequate representation of the arborescent stratum, that is, to approach reality as to the composition and structure of the tree stratum. The immediate goal is not that of crusing the association-individual, or stand, for its merchantable content in board feet or cordage, but the method, if valid, should yield such data with approximately the same limits of error as, for example, basal area, which is used here as the basis for comparison. The system, which is not at all new, is simply that of employing small sample areas (quadrats) on a basis of random sampling within the stand. The study differs from the usual in that an inspection of the influence of size and number of quadrats is made with the purpose of ascertaining the minimum quadrat area and the minimum number of such quadrats which will produce results within certain limits of error.

Ordinary timber cruising methods are based on the strip, usually one chain, or one-half chain, in width.[2] These strips are regularly spaced so as to result in a 10 per cent cruise in most studies of any extent. Sometimes careful notes taken along these lines permit the construction of forest type maps but more often only the broader cover types are indicated, as conifer, hardwood, second growth, burns, etc., or the division may be made on a basis of ridge, slope, cove, etc. Such cruises regularly yield satisfactory commercial results, checking well with mill tallies. The most recent development in forest mensuration is the so-called "line-plot method" which is being used by the Forest Survey.[3] In the Lake States a fifth acre circular plot is taken every ten chains along lines run ten miles apart. From the strips already run it is estimated that the accuracy for the large types in the Lake States will be about 2 to 5 per cent.

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1 Earlier un-numbered contributions to this series by the author are to be found in the Butler Univ. Bot. Studies. **1**(9):129-150. Ibid. **1**:177-208, 1930. No. I is in the Bot. Gaz. **91**:22-41, 1931.

Contribution No. 68 from the Waterman Institute, Indiana University.

2 The *chain* in use for general land surveying is 4 rods or 66 feet long, approximately 20 meters.

3 I am indebted to Dr. Hardy Shirley of the Lake States Forest Experiment Station for this information and for certain other suggestions concerning the manuscript.

In the localized and detailed work for yield tables, foresters regularly employ large numbers of plots of one-fourth to one-half acre in size, which are optimum for the basal area and volume determinations. One plot per stand is taken and as many stands of the type and site as practical are studied. Experienced field men can select the location for a single one-half acre plot so that it is reasonably representative of the average for the site and age class of the type. If one stand only is to be investigated it is apparent that a more accurate result will be obtained on a basis of an equivalent area sampled on a basis of several smaller quadrats. With respect to this point Cain (1934) has shown that in a certain woods 25 quadrats, each 100 sq. m., revealed 83 per cent of the total flora on a basis of 2.5 per cent of the total area. A single one-half acre of 2.0 per cent of the total area of the woods yielded only 57 per cent of the total flora. Also, the basal area results indicated greater accuracy of sampling of the trees, as compared with a 10 per cent strip cruise, on a basis of the small scattered quadrats than by the single one-half acre plot. The author believes that for more extensive investigations than of a single or a few stands the quadrat method would yield more significant results than the single plot method. Such a method also yields information for a more detailed statistical analysis and certain otherwise unobtainable data, as, for example, frequency.

On a basis of the single plot method Ilvessalo (1929) says:

> The sample plot to be investigated must not be too small, for then the variations cannot be taken into consideration sufficiently. A size to be recommended is half an acre. . . Whatever methods are used, the investigation of the vegetation should always the whole time be made according to the same system in the same research and in the same manner, so as to enable all the results to be compared with each other in the right way.

Bruce (1926) discussing timber-yield tables has this interesting suggestion concerning plot size:

> The question of proper plot area is in need of more thorough analysis. The general impression has been that plots should be as large as possible without too great a sacrifice in density of stocking, and that smaller plots are permissable in younger stands. In some studies limits of 0.1 to 1.0 acre have been set. It seems possible that a limitation by area is illogical and that a limitation by number of trees should be substituted. The average number of trees per plot (average plot size 0.24 acre) in the longleaf pine study was 157. On a basis of the composite curve for all sites showing numbers of trees per acre this corresponds to the following area scale:

Age, 10 years	0.09 acres per plot
Age, 20 years	.14 acres per plot
Age, 40 years	.31 acres per plot
Age, 60 years	.46 acres per plot
Age, 80 years	.60 acres per plot
Age, 100 years	.71 acres per plot

A considerable quantity of investigations of statistics of forest (site) types, on size of the sample area, etc. has been produced by the north-European foresters. This work, however, relates mostly to the undergrowth as, following Cajander (1926) and his earlier work, the forest types are based on the field layer rather than on the tree layer. Of especial interest is a paper by

Illvessalo (1922) in which, among other things, he investigates the influence of size and shape of the sample area on the species number. He finds that a stable result is obtained on a basis of a strip with a smaller area sampled than on a basis of a quadrat; also, that the area necessary to be sampled varies with the forest type.

Before proceeding with data from this investigation it is desirable to present a description of the two stands investigated.

The great Canadian spruce-fir forest complex is represented in its southernmost outpost in the East by a magnificent forest in the Great Smoky Mountains National Park of North Carolina and Tennessee. Here the two dominant species are *Picea rubens* Sargent *(P. rubra* (DuRoi) Dietr.) and *Abies Fraseri* (Pursh) Lindl. Small (1933) recognizes also *Picea australis* which, however, the author has been unable to distinguish with certainty from the Smokies. Also, *Picea mariana* (Mill.) B.S.P. is recorded in the literature from North Carolina, but it seems to be absent from the spruce-fir formation of the Great Smoky Mountains.

Spruce, as a dominant or codominant, usually makes its appearance at about 4,500 feet elevation, varying with topography. With increasing altitude Fraser's fir increases in importance in the stand until it becomes a codominant with spruce and finally, around an elevation of 6,000 feet or more, it may constitute 80 per cent or more of the stand. The Society of American Foresters (1932) recognizes the following types in the spruce-fir group of the northern forest in the Southern Appalachians:

Type 16. Yellow Birch-Red Spruce
Type 18. Red Spruce
Type 19. Red Spruce-Southern Balsam Fir.

To the author it seems necessary to recognize an additional type in which *Abies Fraseri* constitutes 80 per cent or more of the stand. This type occurs at higher elevations on the poorest sites. Examples of the Red Spruce Type and the Southern Balsam Fir Type are here investigated and it seems advisable to give them the technical names after the method of the plant geographers which is rapidly becoming standard the world over (Braun-Blanquet 1932). They are *Piceetum rubentis* and *Abietum Fraseri,* respectively, for the spruce and the fir types.

Piceetum rubentis

Red Spruce Forest Type

For this type a location was selected which would represent the spruce in an old-aged stand of fine development. Such a stand is accessible on Mt. Mingus in the vicinity of Indian Gap. The quadrats forming the basis of this study were laid out on the south-facing slope of Mt. Mingus approximately along the 5,100-foot contour line. This forest is illustrated in figures 1 and 2.. The latter is a coverage-stratification diagram (Cain, 1932) showing the coverage in each natural stratum of the community as well as the mean mature height of each stratum. Table 1 lists the species in each

Fig. 1. A view of Piceetum rubentis on Mt. Mingus at 5,100 feet elevation in the region of the quadrat study. Photo by S. A. Cain.

stratum as determined by the sample areas. Table 2 shows the composition of the arborescent strata in terms of basal area and percentage derived from a sampling of approximately 2½ acres. Although red spruce constitutes 88.9 per cent of the total basal area of the stand it forms 100 per cent of the superior arborescent stratum. Southern balsam fir forms only 7.3 per cent of the basal area of the whole stand but nearly 75 per cent of the intermediate stratum, exclusive, of course, of that red spruce which is transgressive in the middle tree layer. The total basal area of the stand is quite high, being approximately 325 sq. ft. per acre.

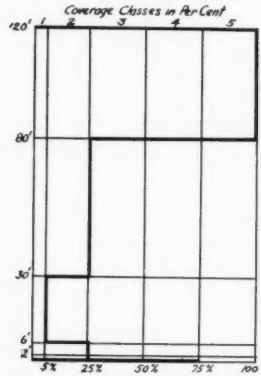

Fig. 2. A coverage-stratification diagram of Piceetum rubentis based on the quadrat survey. The heavy black line on the right indicates the coverage class for each stratum.

In this community deciduous trees, although there are seven species, are widely scattered, but relatively more abundant in the draws, while the spruce is usually pure on the low ridges. Among the shrubs *Rhododendron Catawbiense* (with which may occur *R. minus* Michx. and *Kalmia latifolia* L.) occurs mainly on the ridges. The herbaceous cover is found where reproduction of the trees and the shrub cover do not offer too great competition.

TABLE 1

Stratification of *Piceetum rubentis*, Mt. Mingus, based on the sample areas examined.

I. SUPERIOR ARBORESCENT STRATUM: C 5, 120 ft.
Picea rubens Sargent

II. INTERMEDIATE ARBORESCENT STRATUM: C 2, 80 ft.
Abie Fraseri (Pursh) Lindl.
Betula allegheniensis Britton

III. INFERIOR ARBORESCENT STRATUM: C 1, 30 ft.
Amelanchier laevis Wiegand
Ilex monticola A. Gray
Fagus grandifolia Ehrh.
Sorbus americana Marsh.
Acer spicatum Lam.
Acer pennsylvanicum L.

Fig. 3. A view of the Abietum Fraseri on Mt. LeConte at 6,300 feet elevation in the region of the quadrat study. Photo by S. A. Cain.

IV. SHRUB STRATUM: C 2, 6 ft.
Viburnum lantanoides Michx.
Hugeria erythrocarpa (Michx.) Small
Cyanococcus pallidus (Ait.) Small
Rubus canadensis L.
Rhododendron Catawbiense Michx. (locally, C 5, to 15 ft.)

V. HERBACEOUS STRATUM: C 2, 2 ft.
Thelypteris spinulosa var. *americana* (Fischer) Weatherby
Athyrium asplenioides (Michx.) Desv.
Dennstaedtia punctilobula (Michx.) Moore.
Lycopodium lucidulum Michx.
Senecio Rugelia A. Gray
Solidago glomerata Michx.
Aster acuminatus Michx.
Eupatorium urticaefolium Reich.
Medeola virginiana L.
Monotropa uniflora L.
Oxalis montana Raf.

VI. SOIL STRATUM (cryptogams): C 4, a few inches high.
See Table 3.

TABLE 2

Percentage composition of *Piceetum rubentis* from the basal area on 10,000 sq. m. sampled by 50 plots at 10x20 m. scattered on Mt. Mingus at 5,100 ft. elevation.

Species	Basal area in sq. ft.		Per cent of stand	
Picea rubens	727.95		88.9	
Abies Fraseri	60.37		7.3	
Betula allegheniensis	20.41		2.5	97.7
Amelanchier laevis	3.49			
Ilex monticola	2.06			
Fagus grandifolia	1.75			
Sorbus americana	1.71			
Acer spicatum	.47			
Acer pennsylvanicum	.19	9.67		2.3
Total for 9 species	818.40			100.0

That magnificent spruce grows in this region is attested by data taken from the cruise of the Road Prong tract of the Champion Fibre Co. which includes this slope of Mt. Mingus.[4] From the cruise sheets I have found that approximately 50 per cent of the trees of 18-22 in. d.b.h. contain 4 16-ft. logs; of the trees from 24-30 in. d.b.h. approximately 50 per cent contain 5 16-ft. logs; of the trees 32-36 in. d.b.h. approximately 50 per cent contain 6 16-ft. logs while about 3 per cent would cut 7 logs. These figures are based on 10,000 trees. Scattered trees reach a total height of over 130 ft. and rarely one attains a height of over 140 ft.

4 These data were obtained through the courtesy of the Tennessee Park Commission.

Abietum Fraseri

SOUTHERN BALSAM FIR FOREST TYPE

This type was studied on Mt. LeConte at an elevation of approximately 6,300 feet on a rather gentle north-facing slope. Much of the tract is occupied by a stagnant pole stand with numerous dead trees, standing and fallen. This forest is illustrated by figures 3 and 4. As seen by these illustrations the fir forest forms a great contrast to the spruce forest. Tables 3 and 4 present data comparable to those of tables 1 and 2 for the other type. There is only one distinct arborescent stratum and it is of low stature. The shrub stratum is of uneven distribution and relatively low coverage. A conspicuous feature is the soil cover of mosses, liverworts, and lichens with a coverage in class 5 and nearly 100 per cent. The soil is shallow, rocky, poorly drained, and highly

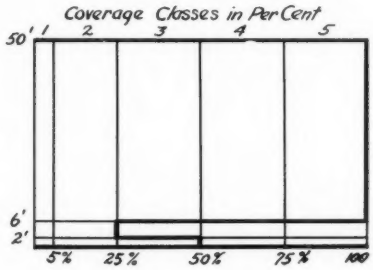

Fig. 4. A coverage-stratification diagram of Abietum Fraseri based on the quadrat survey.

acid. Reproduction is more abundant on fallen logs than on the ground. Table 4 based on two surveys of the same stand shows that *Abies Fraseri* constitutes approximately 90 per cent.

TABLE 3

Stratification of *Abietum Fraseri*, Mt. LeConte, based on the sample areas studied.

I. ARBORESCENT STRATUM: C 5, 50 ft.
Abies Fraseri (Pursh) Lindl.
Picea rubens Sargent
Sorbus americana Marsh.
Betula allegheniensis Britton
Prunus pennsylvanica L. f.

II. SHRUB STRATUM: C 2, 6 ft.
Viburnum lantanoides Michx.
Hugeria erythrocarpa (Michx.) Small
Menziesia pilosa (Michx.) Pers.
Rubus canadensis L.
Diervilla sessilifolia Buckl.
Sambucus pubens Michx.
Rhododendron minus Michx.
R. Catawbiense Michx.

III. HERBACEOUS STRATUM: C 3, 2 ft.
Thelypteris spinulosa var. *americana* (Fischer) Weatherby

Athyrium asplenioides (Michx.) Desv.
Senecio Rugelia A. Gray
Solidago glomerata Michx.
Oxalis montana Raf.
Aster acuminatus Michx.
Monotropa uniflora L.
Chelone Lyoni Pursh.

IV. Soil Stratum (Cryptogams): C 5, height, a few inches.

Bryophytic Synusiae: Spruce-Fir Formation [5]

Terrestrial:

Mosses

A5. *Hylocomium splendens* (Hedw.) Bry. Eur.
A4. *Calliergonella Schreberi* (Willd., Bry. Eur.) Grout
A3. *Polytrichum ohioense* R. & C.
Hylocomium umbratum (Ehrh., Hedw.) Bry. Eur.
Rhytidiadelphus triquetrus (L., Hedw.) Warnst.
A2. *Hylocomium brevirostre* (Ehrh., P. B.) Bry. Eur.
Dicranella heteromalla (L., Hedw.) Schimp.
Webera elongata (Hedw.) Schwaegr.

Liverworts

A4. *Bazzania trilobata* (L.) S. F. Gray
A3. *Lepidozia reptans* (L.) Dum.

Epilithic:

Mosses

A3.	*Sphagnum squarrosum* Pers.	Wet rocks
	S. Girgensohnii Russ.	Wet rocks
	S. imbricatum var. *affine* (R. & C.) Hornsch.	Wet rocks
A4.	*Dicranum fulvum* Hook.	Moist or dry rocks
A3.	*Polytrichum ohioense* R. & C.	Moist or dry rocks

Liverworts

A3.	*Scapania nemorosa* (L.) Dum.	Wet rocks
	S. undulata (L.) Dum.	Wet rocks
	Bazzania trilobata (L.) S. F. Gray	Moist or dry rocks
A2.	*B. tricrenata* (Wahl.) Pears.	Moist or dry rocks

Epixylic:

Mosses

A4.	*Paraleucobryum longifolium* (Ehrh., Hedw.) Loeske (*Dicranum longifolium* Hedw.)	Tree trunks
	Ulota ulophylla Broth. (*U. crispa* of Amer. authors)	Tree trunks
A3.	*Leptodontium excelsum* (Sull.) E. G. Britt.	Tree trunks
	Zygodon rufo-tomentosus E. G. Britt.	Tree trunks
A4.	*Dicranum fuscescens* Turn.	Decaying logs
A3.	*Tetraphis pellucida* Hedw.	Decaying logs

Liverworts

A4.	*Frullania asagrayana* Mont.	Tree trunks
	Herberta tenuis Evans	Tree trunks

5 The author is indebted to Prof. A. J. Sharp, of the University of Tennessee, for this excellent list of Bryophyta and wishes to express his appreciation.

A3.	*Bazzania nudicaulis* Evans	Tree trunks
	Plagiochila tridenticulata Tayl.	Tree trunks
	Mylia cuneifolia (Hook.) S. F. Gray	Tree trunks
A2.	*Microlejeunea ulicina* (Tayl.) Evans	Tree trunks
	Bazzania denudata (Torr.) Trev.	Tree bases
A4.	*Sphenolobus Michauxii* (Web.) Steph.	Decaying logs
	Bazzania trilobata (L.) S. F. Gray	Decaying logs
A3.	*Blepharostoma trichophyllum* (L.) Dum.	Decaying logs

Abundance designations are according to the common system recommended by Braun-Blanquet: Abundance class 5 (A5)=species very abundant in the community; A4=species abundant; A3=species not very abundant; A2=species rare; A1 =species very rare in the community.

The following species, in the Southern Appalachian Mountains, are practically limited to the spruce-fir formation:

Hylocomium splendens Br. eur.
H. umbratum Br. eur.
Rhytidiadelphus triquetrus Warnst.
Bazzania tricrenata (Wahl.) Trevis
Paraleucobryum longifolium Loeske
Bazzania nudicaulis Evans
Sphenolobus Michauxii (Web.) Steph.
Bazzania denudata (Torrey) Trevis.

The following species, in North America, are endemic to the spruce-fir formation:

Plagiochila tridenticulata Tayl.
Mylia cuneifolia (Hook.) S. F. Gray.

The following species are endemic to the Southern Appalachian Mountains and are practically limited to the spruce-fir formation:

Zygodon rufo-tomentosus E. G. Britt.
Leptodontium excelsum (Sull.) E. G. Britt.

The following Cladoniae were collected and kindly contributed by Miss Margaret Fulford of the University of Cincinnati. All specimens have been determined by Dr. A. W. Evans of Yale University. They are listed in approximate order of abundance.

Cladonia squamosa (Scop.) Hoffm.
soil, top of Mt. LeConte
logs, Mt. Mingus
tree base, Mt. Mingus
Cl. squamosa f. *muriana* Scriba
log, top of Mt. LeConte.
Cl. squamosa f. *denticola* (Hoffm.) Floerke
soil, top of Mt. LeConte
Cl. mitis Sandst.
soil, top of Mt. LeConte
Cl. gracilis var. *dilitata* (Hoffm.) Vainio
soil, top of Mt. LeConte
Cl. tenuis (Floerke) Harm. p.p.f. *setigera* Sandst.
soil, top of Mt. LeConte
Cl. furcata (Huds.) Schrad.
soil, Mt. Mingus
Cl. furcata var. *racemosa* f. *arbuscula*
logs, Mt. Mingus
Cl. furcata var. *racemosa* f. *squamulifera* Sandst.
logs, top of Mt. LeConte

Cl. coniocrea (Floerke) Spreng
log, top of Mt. LeConte
Cl. strepsilis (Ach.) Vainio
log, top of Mt. LeConte.

TABLE 4

Percentage composition of *Abietum Fraseri* on Mt. LeConte at 6,300 feet elevation, based on two surveys.

Species	10 quads, 10 x 20 m.		50 quads, 5 x 10 m.	
	Basal area in sq. ft.	Stand percent.	Basal area in sq. ft.	Stand percent.
Abies Fraseri	126.71	87.8	161.43	90.7
Picea rubens	8.08	5.6	7.58	4.2
Sorbus americana	6.12	4.2	5.32	2.9
Betula allegeheniensis	2.57	1.8	2.38	1.9
Prunus pennsylvanica	.72	.6	1.26	.7
Total for 5 species	144.20		177.97	
Total per acre	291.79		288.10	

Procedure

In the Piceetum the quardats were scattered at regular intervals along the 5,100-foot contour line, extending in a westerly direction for over a mile from Indian Gap. In the Abietum the quadrats were regularly scattered in a checkerboard pattern, mainly to the north and northeast of Camp LeConte at about 6,300 feet elevation. In both forests the first 10 stations were sampled by quadrats of different sizes. In the Abietum quadrats of five sizes were laid out at each station as follows: 25, 50, 75, 100, and 200 sq. m. Each larger size included the preceding smaller quadrats. In the Piceetum the same sizes were used with the addition of a set of 400 sq. m. plots. The spacing between the stations was in both instances 40 meters, or 20 meters between boundaries of the largest quadrats. The data from these preliminary quadrats allowed a decision as to the minimum quadrat area to be used in further sampling. This minimum quadrat area proved to be 200 sq. m. for the Piceetum and 50 sq. m. for the Abietum, as is explained later. Subsequently more quadrats were laid out and tallied until a total of 50 quadrats of the minimum quadrat area had been obtained for each forest type.

Results

PICEETUM RUBENTIS

The first phase of the study was concerned with the influence of quadrat size on the sampling of the community. Each size of quadrat for each of ten stations was tallied separately, i.e. as the size of the quadrat was increased the additional trees were added to the previous results for each station. In this manner it was possible to study the frequency of each species for each survey using a different size of quadrat. See Hanson and Love (1930) and Cain (1934). This information for the frequency of each species is presented in

Table 5. Here also is found the average frequency for all species, the average species density per quadrat, and the total number of species per survey based on the different quadrat sizes. These data are plotted against the quadrat area, figure 5, to produce species-area curves which give indication of the minimum quadrat area. From these curves one may conclude that the use of a larger sample area than 200 sq. m. would not increase greatly the validity or accuracy of the data, at least in proportion to the additional labor involved. For the use of such curves see Ilvessalo (1922) and others cited above.

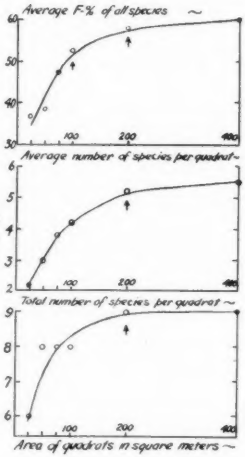

Fig. 5. Species-area curves for the Piceetum rubentis based on the preliminary quadrat surveys employing different sizes of quadrats. These curves indicate 200 sq. m. as the minimum area quadrat.

The next step consisted of an examination of the effect of increasing the number of minimum area quadrats. The results are set forth in Table 6 where the means and other statistical data are presented on a basis of 10, 20, 30, 40, and 50 minimum area quadrats (each 200 sq. m.), on a basis of the basal area of spruce and the associated species for the given number of plots. In this table S.D. is the standard deviation and M_E is the probable error of the mean. The last column of figures (L%) in each section is the "limit of accuracy" selected as three times the probable error of the mean and expressed as percentage of the mean. With this limit of accuracy the odds are approximately 20 to one that the true value falls within these limits. On this basis the limit of accuracy falls from 17.6 per cent for only 10 quadrats to 8.1 per cent for 50 quadrats when only spruce is considered. When all species are considered the percentages are somewhat lower.

It should also be noticed in Table 6 that the standard deviation remains practically constant with an increase in number of samples which is an indication of the proper size of plot and proper sampling of the community in question, i.e. that even 10 plots are a true sample of the 50 plots.

It would seem that this method of sampling would enable an investigator to know when he has sampled a sufficient area within a type. In general it can be said that if only one or a few stands of the type are to be investigated sufficient quadrats should be taken to result in a rather low percentage of error. If, however, several stands of the same type are to be investigated one might well be satisfied with a higher percentage of probable error, that is, within each stand. Each investigator must set his own standards for intensive and extensive work determined by the purpose and time allowable for the field

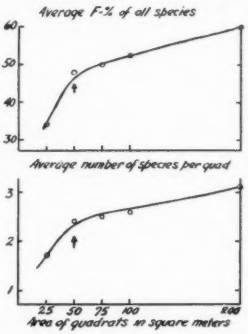

Fig. 6. Species-area curves for the Abietum Fraseri based on the preliminary quadrat surveys employing different sizes of quadrats. These curves indicate 50 sq. m. as the minimum area quadrat.

work. At any rate, one is not sampling "blind" by the quadrat method but has a means of ascertaining his probable error.

Abietum Fraseri

Tables 7 and 8, for the Southern Balsam Fir Type, present data comparable to tables 5 and 6 previously described. Figure 6 is directly comparable to figure 5. It seems unnecessary to add any comment here.

Table 5

Frequency of tree species in *Piceetum rubentis*, Mt. Mingus, obtained from ten plots each of six sizes.

Species	Plot area in sq. m.					
	25	50	75	100	200	400
Picea rubens	100	100	100	100	100	100
Abies Fraseri	60	70	100	100	100	100
Betula allegheniensis	10	20	30	50	70	80
Fagus grandifolia		10	30	40	60	70
Ilex monticola	20	50	60	60	60	60
Amelanchier laevis	20	20	20	30	60	60
Sorbus americana	10	30	30	30	30	30
Acer spicatum		10	10	10	30	30
Acer pennsylvanicum					10	10
Average F - %	36.6	38.7	47.5	52.5	57.8	60.0
Average no. spp. per plot	2.2	3.0	3.8	4.2	5.2	5.5
Total no. spp. per set	6	8	8	8	9	9

TABLE 6

The influence of increasing numbers of minimum area quadrats on the probable accuracy of sampling virgin *Piceetum rubentis* at 5,100 feet elevation on Mt. Mingus.

No. plots at 200 sq. m.	Picea rubra					All species				
	AV.B.A.	S.D.	M_E	E%	L%	AV.B.A.	S.D.	M_E	E%	L%
10	14.95	±4.12	±.88	5.9	17.6	16.75	±4.03	±.86	5.1	15.3
20	13.24	±4.67	±.70	5.3	15.9	15.42	±4.60	±.69	4.5	13.5
30	13.46	±4.10	±.51	3.7	11.1	15.89	±4.29	±.53	3.3	9.9
40	14.12	±4.41	±.48	3.4	10.2	16.18	±4.36	±.46	2.9	8.7
50	14.56	±4.18	±.40	2.7	8.1	16.38	±4.03	±.38	2.3	6.9

TABLE 7

Frequency of tree species in *Abietum Fraseri*, Mt. LeConte, obtained from ten plots of five sizes.

Species	Quadrat sizes: sq. m.				
	25	50	75	100	200
Abies Fraseri	100	100	100	100	100
Sorbus americana	30	70	80	80	80
Picea rubens	20	30	30	40	50
Betula allegheniensis	10	30	30	30	40
Prunus pennsylvanica	10	10	10	10	30
Average F - %, all species	34	48	50	52	60
Average no. spp. per plot	1.7	2.4	2.5	2.6	3.1

TABLE 8

The influence of increasing numbers of minimum area quadrats on the probable accuracy of sampling in virgin *Abietum Fraseri* at 6,300 feet elevation on Mt. LeConte.

No. plots at 50 sq. m.	Abies Fraseri					All species				
	AV.B.A.	S.D.	M_E	E%	L%	AV.B.A.	S.D.	M_E	E%	L%
10 [6]	3.74	± .91	±.19	5.2	15.2	4.32	± .96	±.20	4.7	13.9
20 [6]	3.34	± .90	±.14	4.1	12.6	3.75	±1.01	±.15	4.1	12.0
30	2.96	±1.14	±.14	4.8	14.2	3.34	±1.21	±.15	4.4	13.7
40	3.23	±1.15	±.12	3.8	11.1	3.56	±1.17	±.12	3.5	10.1
50	3.23	±1.09	±.10	3.2	9.3	3.76	±1.17	±.11	3.0	8.8

6 It is evident that the samples consisting of 10 or 20 plots are not true samples of the 50 plots since the standard deviation is too low, not having reached a constant.

Discussion

Plant sociology (phytocoenotics) is a morphological science having as its goal the accurate description and delimitation of plant communities. The more complex plant communities (phytocoenoses) are exceedingly difficult to describe in generalities and for purposes of comparison one needs more than rhetoric, no matter how careful the writers' diction. Especially one is embarrassed by idioms and exact adjectival meanings in foreign languages. Plant geographers (including plant sociologists, ecologists, foresters, et. al.), especially within the present century, have been developing concepts of a quantitative nature together with methods for their ascertainment. Students of plant communities find themselves confronted with two aspects of the problem; that of the community individual (in the concrete), and that of the community in the abstract, as synthesized from a study of several different, yet similar, community individuals. These synthetic studies lead naturally to matters of community classification and distribution. Since one gains knowledge of a community from the exact description of the community individual and from repeated examples of the same or related communities from different locations the time and labor involved in the field work becomes great. It, therefore, would seem wise to examine these methods with the goal of reducing the field work to the minimum compatible with results adequate to the purpose of the investigation. Thus the investigator will have time for the study of an increased number of community individuals. It is thus one gains confidence in the validity of the community under investigation. The same pitfall lies before the student of plant communities that entraps the species taxonomist who describes a *species nova* from a single herbarium sheet or locality. The taxonomist of species may have hold of a restricted ecotype. The student of the community may be analysing a geographical variant or a facies of chance composition.

The present investigation was actuated by the desire of the writer in the future to make a comparative study of the spruce-fir forest type group as found disjunct along the Appalachian Mountains and in its transcontinental, boreal zone. If any such ambitious program is to be consummated, as little time as possible must be spent on any individual stand.

One has also in the quadrat method an opportunity to treat the derived data statistically and thus to obtain some indication of the probable accuracy of the results, as one deals with numerous samples taken (as a random sample) in the statistical universe. The qualitative basis for the comparison in the present study is basal area. In so far as the arborescent stratum, or strata, of the more complex communities is concerned, one might as well use data of more immediately practical import as cubic volume, board feet, or cordage, except for the additional labor of determining merchantable height. For the non-arborescent strata, which are not dealt with in the present study, one might treat statistically density, coverage per cent, or some other aspect of the species composing the vegetation as, for example, per cent of character species.

For commercial timber cruising as well as for the more academic investigations of the plant sociologists, it would seem that the quadrat method might

hold advantages over the customary strip method or the single plot method. A specific illustration of the principle involved in this type of forest mensuration is in a brief paper by Preston (1934). He used a sample plot of 1/4 acre, first determining the area of each type to be cruised and then the necessary number of plots to reduce the average stand per acre to a percentage of probable error consistent with the time allowed for the cruising and value of the stand. It is perhaps worth while to quote:

> Following are some notes to show how the combination of the old methods, slightly changed, with the newer science of statistical analysis, has added new interest, reduced effort, and improved accuracy of the old foundation job of forestry . . . . The problem is to change the system so as to bring about the desired result . . . . First, a plan to enable the cruiser to arrive at his estimate of stand per acre while he is in the woods and looking at the identical trees for which he is calculating the volume. Second, statistical analysis of his results day by day, so that he knows when he has sufficient plots for a fair figure of average stand for each type, consistent with the amount of money he has to spend and the use to be made of his results. We are beginning to learn the futility of adhering to a 5 or 10 per cent cruise or some other fixed, preconceived standard of area to be covered by the cruise. The modern idea is to recognize and map the timber types (the area factor) and then take enough samples in each type to satisfy the purposes of the cruise (the stand factor).

This is essentially the principle of the quadrat method and was used in this case for a cruise of approximately 3,000 acres divided among six area types: Black spruce, white spruce, Jack pine, popple, cedar, and unmerchantable. The first three types constituting about 2/3 of the total tract were cruised by the method. In the quadrat method, with smaller plots and a considerably smaller total area sampled, it would be feasible further to subdivide forest types into sub-types, transition types, and site types. The major difficulty arises not from the details of the sampling but in the recognition and delimitation in the field of the smaller forest units. Yet, it is on this basis that the statistics from the quadrat surveys take on their validity and accuracy with greater speed, i.e. on a reduced sampling area. As Raunkiaer (1934) has adequately demonstrated in his various researches, vegetational statistics have the greatest significance when they are derived from the smallest and most homogeneous plant communities, i.e. when the plant community is taken in its narrowest concept. It is true, of course, that it takes longer to cruise an acre when it is divided into relatively small quadrats than it does to cruise it on a chain-wide or half chain-wide strip, or by 1/4 acre plots. The saving of time results from the much smaller percentage of the tract which has to be cruised. Or even if no material saving of time should result, forest mensuration when carried on by the method suggested by Preston (1934), or by the quadrat method, yields much information otherwise unobtained and valuable in silviculture as well as to the non-commercial botanist interested in community structure, distribution, ecology, etc. At present, without further study, it would seem that Preston's method by the use of larger plots is more suited to most timber cruising than the quadrat method. Even in some plant sociological investigations of tree layers, for the distinction of forest stand types, for example, the use of larger plots (1/4 acre or more) may be more efficient than that of small scattered quadrats.

The north-European forest (site) type method as developed by Cajander and others is recently being studied by American investigators at Yale, Syracuse (Heimburger, 1934), and elsewhere. Such studies will rapidly force our foresters to a consideration of the methods and broader vegetational concepts of such workers as Cajander, Gams, Du Rietz, Braun-Blanquet, et al., as their forest types are based on several strata of the forest community and not on the tree stratum alone. As Gams (1933) recently emphasized:

> The ideal of scientific vegetational study remains, of course, the equal study of all communities (all layers and synusiae) . . . . a goal which can perhaps rarely be accomplished in applied vegetational science because the erection and description of forest types . . . . can be undertaken only by a plant geographically trained forester or a geographer sufficiently trained in forestry with a practical slant . . . .

Each forest is composed of several to many stands (layers, synusiae) but for practical purposes the useful division can only be made according to a few. Either according to the woody stands (as in America, central Europe. etc.) or those of herbs, shrubs, or mosses. To employ all layers in the characterization of forest types would confuse matters too greatly for applied science, yet to construct a forest type and site system on the tree layer alone is inadequate. We, too, will undoubtedly find the characterization at least of site classes within the forest types conveniently made on a basis of certain critical species of the inferior layers. That is, we will find that site classes are indicated by certain species or species combinations of herbs, shrubs, mosses, lichens, etc. as already demonstrated for northwestern America by Ilvessalo (1929), and for the Adirondack region by Heimburger (1934).

The Continental use of the word "stand" to refer to any concrete example of a plant community whose species are of similar life-form (as, a stand of epixylic or epilithic mosses and lichens, a stand of herbs, etc.) is rather strange to us who apply it to the whole complex (phytocoenosis), tree, shrub, herb layers, etc., or to the tree layer alone. Cajander (1922) has set forth some definitions which prove of interest:

> *Settlement* (Siedlung), a uniformly varying more or less embracing portion of the plant cover which is locally characterized as a distinct whole, for example, a Pinetum silvestris callunosum.[7]

> *Stand* (Bestand), a more or less independent part of a settlement (Siedlung), for example the superior stand, the moss stand, the epiphyte stand, the bacteria stand, etc. of a definite homogenous oak forest settlement. The stand can be pure or mixed.

Long practice has established the term "stand" of timber to refer primarily if not exclusively to the component tree species. Increasing recognition of the importance of associated "stands" of shrubs, herbs, mosses, etc. in forest community studies will force the extension of that term to include what is meant by "Siedlung" as well as what is meant by "Bestand," or the adoption of some such term as "settlement" for the complex of plant communities which compose the forest as represented by any concrete example.

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[7] (That is, a forest of *Pinus silvestris* with a distinctive undergrowth of *Calluna vulgaris* together with all other associated layers and synusiae.)

Summary

1. A brief description is given of examples of two forest types in the Great Smoky Mountains National Park: The Red Spruce Type *(Piceetum rubentis)* and the Southern Balsam Fir Type *(Abietum Fraseri)*.

2. A method of sampling the arborescent strata (similar to that widely in use for non-arborescent communities is described.

a. The method is based on a random sample by minimum area quadrats.

b. The minimum area quadrat is determined for each community type by the form of species-area curves.

c. The surveys based upon different numbers of minimum area quadrats are compared statistically by use of basal area data to determine the necessary number of quadrats to be investigated.

d. It is suggested that the quadrat method may be applicable to commercial cruising if applied on a basis of sub-types and site classes.

e. Forest types, sub-types, and site classes will probably be found to be characterized by certain species inferior to the tree layer, although the present paper does not contain definite investigations of that aspect.

3. It is thought that *Abies Fraseri* must be recognized as forming, in the Great Smoky Mountains at least, a forest type in which it is the sole dominant.

ACKNOWLEDGEMENT

The author wishes to express his deep appreciation for the Waterman Institute of Indiana University which has made possible this and other investigations since June, 1933. He wishes also to express his gratitude for the many aids and privileges afforded him by the officials of the Great Smoky Mountains National Park; to Mr. Willis King, Park Naturalist-Technician, who has assisted him in the field, and to Mr. Jack Huff, with whom he stayed on Mt. LeConte.

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PALEOBOTANICAL EXAMINATIONS OF CRETACEOUS AND TERTIARY COALS

ERNEST L. MINER

I. CRETACEOUS COALS FROM GREENLAND*

Introduction

The studies that have been made on the plant remains in coal are in no way comparable to the work that has been done on the fossil plants from other sedimentary deposits. The fine collection of Western Greenland coal, made by Mr. Carl O. Erlanson in 1928, was made available to the writer for examination. It has been dealt with in a preliminary way by Arnold (1932), and the writer has previously published descriptions of several new species from megaspores (Miner, 1932). This present paper classifies and discusses in more detail the relationship, geological age, and distribution of this coal flora.

A survey of the literature dealing with the paleobotany of coal reveals the fact that nearly all the studies made, whether microscopic or otherwise, deal more with the origin and structure of coal than with the identification and classification of the plants that contributed to the various coal beds. Those desiring a more complete and detailed discussion of the history of the microscopic examination of coal are referred to Thiessen (1913, 1920). Only those workers who have attempted to identify and classify the plant fragments seen in coal will be mentioned in this study.

Historical

Various ingenious methods for the microscopic study of coal have been employed. Witham (1833) was perhaps the first to make a microscopic investigation of coal and the first to use thin sections. He observed and illustrated cellular tissue which he considered to be of vascular plants, some of which was coniferous or phanerogamic in structure. Evidently some of the cell structures that he observed were merely cross sections of spores, as shown by the illustrations of his sections of cannel coal. Of special interest were the sections from a piece of coal that showed tissues of a plant which he thought resembled the recent Coniferae, and which he named *Pinites carbonaceus*.

Dawson (1859, 1863, 1866, 1871) studied quite extensively over a period of several years the composition of Nova Scotian coal; and while engaged in examining shale, shaly coal, and coal he observed rounded bodies for which the name *Sporangites* was proposed. He considered them "spore-cases" of *Lepidodendron, Calamites,* or similar plants. The exact nature and structure of Dawson's *Sporangities* is not clearly understood or known.

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* Papers from the Department of Botany and Herbarium of the University of Michigan, No. 459.

Probably the best early descriptions and illustrations of spores, spore appendages, cuticles and various other plant fragments found in coal, ranging in age all the way from the Devonian to the Tertiary, were given by Reinsch (1884). He figured over five hundred spores referred to as *Trileteae* and interpreted them as Algae or algoid plants. The "tribe" *Trileteae* is composed of the single genus, *Triletes,* and Reinsch characterized the species by numbers rather than by specific names. He regarded the appendages of the spores as distinct parasitic organisms and described them as such. He included a variety of cuticles under *Stolidermieae.* In his interpretations he was led astray by erroneous conceptions regarding the true nature of plant fossils in coal.

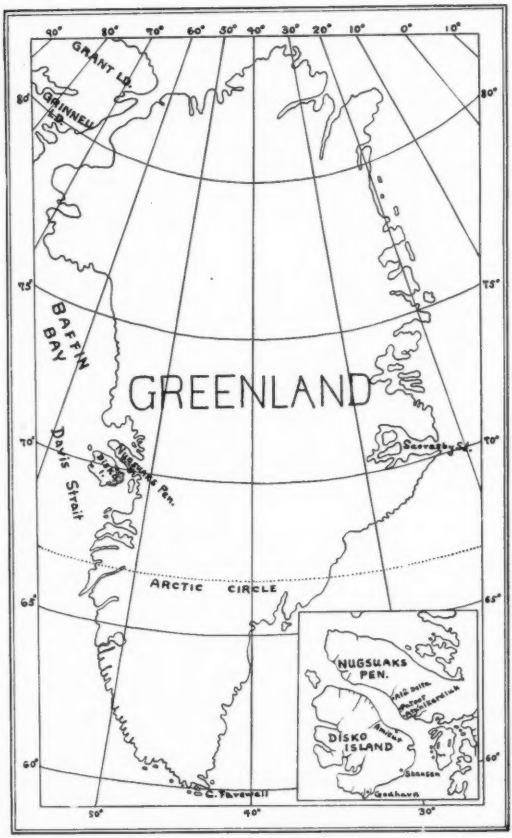
Bertrand and Renault (1892) found in Boghead coal some small plant bodies which they considered to be algae and instituted the genus *Pila* for them. Later (1893) while engaged in studying similar coals and oil shale they observed other alga-like bodies for which they formed the genus *Reinschia.*

Like most of the earlier workers, the recent investigators have also been primarily interested in the structure or origin of coal. The more recent investigations may then be grouped into two classes, those primarily concerned with the structure or origin of coal, and those with the plant remains recovered from coal; although both recognize the importance of fossils for stratigraphical purposes. In the latter group there are the excellent paleobotanical studies of Bartlett (1929), Zerndt (1930a, 1930b, 1931), Potonié (1931a, 1931b, 1931c), and Kirchheimer (1930, 1931a, 1931b). These investigators used the maceration process and were able to isolate a great variety of megaspores and microspores. The various spores were named and described, and their relationships or affinities indicated wherever it was possible to do so.

Geological Age of the Greenland Coal

All the coal examined in the present studies appears to be Upper Cretaceous, as is indicated by the paleontological and stratigraphical work of various investigators. The sedimentary rocks of Western Greenland are mainly sandstone and shale with a few layers of coal. The coal beds are lenticular and vary in thickness from a few inches to several feet (Ball, 1923, Bøggild, 1928). The series of rocks in which they occur is about 3,500 feet thick (White and Schuchert, 1898), and ranges in age, without stratigraphic break, from the Lower Cretaceous to the Eocene. From a study of the plant fossils contained in these rocks Heer (1882, 1883) recognized four floras, the Kome or Neocomian, Atane or Cenomanian, Patoot or Senonian, and Atanikerluk or Miocene. This last division is now referred to the Eocene (Bøggild, 1917, 1928). Berry (1925) states that subsequent work on this Cretaceous flora has shown that the boundaries of Heer's units were largely arbitrary, although the main bodies of his floras are quite distinct.

The Kome series is best developed on the north side of the Nugsuaks Peninsula. The flora of this series as a whole is considered similar to that of the Potomac formation by White and Schuchert (1898). No coal from the Kome series was included in the present study.



Map 1. Map of Greenland showing the position of the region studied. This region is indicated by the shaded area. The insert is a more detailed map of this region, giving the principal localities where coal was collected. Modified from Danish government maps, Copenhagen. (Bøggild 1928; K. J. V. Steenstrup 1888).

The Atane series has the widest distribution, occurring over almost the entire area, on the north side of Disko Island, the north and south sides of the Nugsuaks Peninsula and Upernivik Island. From paleobotanical evidence White and Schuchert (1898) state that this series is closely correlated with the Amboy calys, but the faunal evidence indicate that it is to be correlates with the Fox Hills sandstone or the Pierre shale of the Montana group.

The Patoot series is higher than the Atane and lithologically and stratigraphically inseparable from it. At the locality called Patoot this series commences at about 500 feet above sea level and extends upwards over 2,000 feet, where it passes into the Tertiary (White and Schuchert 1898). From a study of the invertebrate fauna contained in this series Loriol (1893) classified it as Senonian in age and this conclusion is supported by the later works of Ravn (1918). Berry (1925) shows that the flora has many features in common with the Dakota, Raritan, Magothy, Ripley and Atane floras. Seward (1925, 1927), after making a critical study and revision of the Cretaceous floras of Western Greenland, concludes that a more thorough study of the section is necessary, because with the available facts it is difficult to correlate them accurately with other regions. He also expresses the opinion that these floras represent more fully than any others the early stages in the transitional period from an older Jurassic-Wealden vegetation to the type that continued into the Tertiary.

On Disko Island the Cretaceous-Tertiary boundary has not been determined. However, at Skansen, Seward (1927) examined Cretaceous strata at an elevation of 1,900 feet. The highest collection made on this island by Erlanson was at approximately 1,380 feet, and the highest made on the Nugsuaks Peninsula was at Patoot at a height of about 1,248 feet. It is apparent, therefore, that all the collections were made at levels well within the boundaries of the Upper Cretaceous as given by Seward (1927), and White and Schuchert (1898).

Methods

In this study the maceration method alone was used as it is the most satisfactory one for the study of the isolated and fragmentary plant remains, such as spore exines, seeds, cuticles, charcoal, etc., recovered from coal.

Schulze (1855) was the first to adapt to lignite and bituminous coal the maceration process used in the separation and isolation of anatomical elements in living plants. His method has since been variously modified by different workers. The principles for the procedure followed here were those given by Bartlett (1929).

The coal was macerated and prepared for microscopic examination by soaking it first in dilute nitric acid (5-10%) for a period of several months to a year, depending on the kind of coal. Then it was washed in water to remove the acid, and placed in a dilute sodium hydroxide solution (2%) for a few days or until the maceration was complete. The resulting brown liquid was washed out with water, leaving a residue of (a) mineral inclusions, such as sand, (b) organic remains such as spore exines, seeds, cuticles, charcoal,

resin, etc. This residue was examined under a binocular microscope and the various fragments removed. These plant fossils, with the exception of large pieces of charcoal and large seeds, were mounted in euparal (Miner, 1932).

The charcoal was embedded in paraffin by the butyl alcohol process and cut on a rotary microtome in serial sections 15-25μ in thickness. Transverse, radial, and tangential sections were cut from each specimen. The charcoal sections were mounted on slides without removing the paraffin as the material would disintegrate if the paraffin was removed. This necessitated the use of a mounting medium which did not contain a solvent of paraffin. Euparal was satisfactory. To leave the embedding matrix in the material, as is sometimes done with material embedded in celloidin, did not appear to affect the transparency of the sections. Some samples did not yield any pieces of charcoal large enough to be sectioned, so the small fragments were teased apart and then mounted.

"Smear" mounts were made of the finer plant debris in which particles were too small to be examined with a binocular microscope. The material for the "smear" mounts was collected at the time the sodium hydroxide was washed from the samples, as the water from the washing process was charged with fine plant remains. After the material had been allowed to settle, the excess water was decanted and the residue mixed with a suitable mounting medium, such as brown glucose ("karo") syrup or glycerin jelly. The syrup mixture was then gently heated until it became of proper consistency for mounting. For this method of recovering minute plant tissue from macerated coal the writer is indebted to Professor H. H. Bartlett.

Policy with Regard to Naming Fossils of Undetermined Affinity

A successful treatment of such isolated plant fragments as occur in coal necessitates the use of names for spore exines, cuticles, seeds, etc., regardless of whether or not their affinities and relationships are known. Thiessen (1920) is opposed to giving definite names to such fossils without knowing their affinities, but yet he shows quite convincingly that they are stratigraphically significant and that correlations may be established through comparison of the characteristic fossils. Zerndt (1930a, 1930b, 1931) gives definite names to isolated spores, because he also finds that it is possible to differentiate the various strata with the aid of such spores. He places the megaspores in the form-genus *Triletes*. Potonié (1931a, 1931b, 1931c) in his studies on lignite, uses for the various small spores and pollen grains, such generic names as *Sporonites, Pollenites,* and also such compounds as *Piceae-pollenites, Tiliae-pollenites, Gossippii-pollenites,* and *Polypodii-sporonites*. The form-genera *Sporonites* and *Pollenites* are for small spores and pollen grains of unknown affinity, and the other generic designations are for pollen grains or small spores the affinities of which are known and are indicated by the generic name.

It seems, that if a fossil is distinctive enough to be used in determining correlations it should have a specific name. If such a fossil is not named it can not be included in indexes, nor can it be conveniently referred to in the literature, so as a result the original record of it is soon lost to science. In

this connection it must be remembered that although biological science does not consist entirely of names, yet progress is difficult without them.

Enumeration of the Plants

Bryophyta

Chrysotheca gen. nov.

Plant body small, smooth, ovate, oblong-ovate, or lanceolate, with few to several plications, sessile or apparently short stalked; mouth fringed or slightly laciniate.

Chrysotheca diskoensis sp. nov.

Plant body smooth, ovate, oblong-ovate, or lanceolate, 232-348 x 680-1029μ, generally 280 x 796μ, 3-6 plicate to the base, sessile or apparently short stalked; mouth slightly fringed. Amisut, east coast of Disko Island, Greenland; Upper Cretaceous. Plate 18, Figures 1-10. Walton (1925, 1928) instituted the form-genus *Hepaticites* for fossil plants that give evidence of a relation to living *Hepaticae* and of the characteristics which distinguish them from the other divisions of the plant kingdom. The genus is based upon the vegetative remains of some Carboniferous liverworts, resembling the thalli of the anacrogenous *Jungermanniales*. He also shows that of the many fossil organisms described under generic names suggesting affinities to the *Hepaticae*, only a very few afford any reliable information concerning this group. The genus *Chrysotheca* is based upon plant remains which resemble the perianths of many of the *Jungermanniales*. The specimens are rather delicate sack-like structures varying in shape from ovate to lanceolate, with 3 to 6 plications or longitudinal furrows extending from the base to the apex and converging at the mouth or apical opening. The mouth is apparently fringed or slightly laciniate. Cotypes. Slides No. 15455, 15456, Museum of Paleontology, University of Michigan.

Lycopodiales

The following species, *Selaginellites Erlansonii, S. papillosus, S. greenlandicus, S. echinatus, S. borealis, S. inornatus, S. subrotundus, S. Ariadnae,* and *S. Arnoldii,* were recovered from this coal and previously discussed (Miner, 1932). Further examination of the coal has not given any new locality records, except for *S. Arnoldii.* This species besides occurring in the coal from Skansen, east coast of Disko Island, two miles inland at an altitude of 140 meters, and at Patoot, southeast coast of Nugsuaks Peninsula, at an elevation of 165 meters, has also been found in the coal from the latter locality but at a height of only 85 meters. A specimen is illustrated on Plate 18, Figure 22. Slide No. 15466, Museum of Paleontology, University of Michigan.

Filicales

Thecopteris gen. nov.

Small, or medium-sized fern sporangia, annulus vertical and incomplete,

sometimes indistinct; spore masses compact, circular or nearly so; spores small, deltoid, numerous.

Thecopteris major sp. nov.

Sporangia 415 x 498μ in diameter; annulus apparently vertical and incomplete, sometimes indistinct, exact position of the stomium uncertain; spore masses orbicular or nearly so, slightly smaller than the sporangia; spores deltoid 25-35μ in diameter, numerous. Skansen, east coast of Disko Island, Greenland; two miles inland at altitude of 385 meters; Upper Cretaceous. Plate 18, Figures 11-15. Cotypes. Slides No. 15460-15463, Museum of Paleontology, University of Michigan.

Thecopteris minor sp. nov.

Sporangia 315-398μ in diameter; annulus indistinct, position of stomium uncertain; spore masses slightly smaller than sporangia, usually more or less orbicular; spores deltoid, 35-45μ in diameter, numerous. Skansen, east coast of Disko Island, Greenland; two miles inland at an altitude of 385 meters, and one mile inland, at an elevation of 175 meters; Upper Cretaceous. Plate 18, Figures 16-19. In this species and the preceding one the spore masses, without the sporangia, were much more abundant than those with the sporangia. The sporangium and its annulus apparently disintegrate quite rapidly. The exact relationship of this fern are rather difficult to determine from the information available. If the annulus can be interpreted as being equatorial, then these resemble the *Gleicheniaceae*, but if the annulus is vertical and incomplete as it apparently appears to be then they show a closer affinity to the *Polypodiaceae*. Cotypes. Slides No. 15460, 15462, 15464, Museum of Paleontology, University of Michigan.

CONIFERALES

Cedroxylon sp.

Transverse.—Tracheids square to hexagonal, rather large but variable in size. Growth rings distinct. Rays narrow. No resin canals or wood parenchyma visible.

Radial.—Bordered pits uniseriate, separate or contiguous; circular or slightly flattened when contiguous. Ray cells with one or two simple, circular or elliptical pits per tracheid. No ray tracheids, or resin canals determinable. Bars of Sanio absent.

Tangential.—Rays narrow, apparently uniseriate and 4-15 cells high. Skansen, east coast of Disko Island, Greenland; two miles inland at an altitude of 140 meters; Upper Cretaceous. Plate 20, Figures 67-69; Text Figure 1. Slide No. 15502, Museum of Paleontology, University of Michigan.

The form-genus *Cedroxylon* is used here as defined by Bailey (1933) in his recent investigations on the range of structural variability in certain recent and Mesozoic coniferous woods. No vertical resin canal could be detected in the transverse section which has approximately an area equal to about one

fourth of a square inch. The bordered pits occur on the radial walls of the tracheids and are of the type shown in Text Figure 1. The separately spaced pits (Text Figure 1, a, d, e, Plate 20, Figure 69) were the most common ones observed. The contiguous bordered pits (Text Figure 1, b, c.) with the sides slightly flattened at point of contact were observed quite frequently. The tracheid pitting thus shows abietinous and araucarian characteristics, with the former predominating. At no time were any structures seen that could be interpreted as bars of Sanio. The apparent absence of them might be attributed to the charred condition of the wood, but this hardly seems possible as I have observed them in charcoal from Montana coal. The ray tracheids and horizontal resin canals, if present, may have been obscured during fossilization.

Cedroxylon spp.

One of two specimens from Skansen, two miles inland at an altitude of 385 meters, showed three growth rings (Plate 20, Figure 70) and tracheids with bordered pits arranged as shown in Text Figure 2; the other had two growth rings and tracheid pitting as illustrated in Text Figure 3. No doubt both specimens belong to the same species as their pitting is only slightly varied. The bordered pits are oval in shape, separate and arranged in one or two vertical rows; those in two vertical rows vary from opposite to alternate. No bars of Sanio are present. The wood rays are apparently uniseriate and probably 2-8 cells high. Slides No. 15503, 15504, Museum of Paleontology, University of Michigan.

A specimen from Skansen, one and one-half miles west and one and one-half miles inland, at an altitude of 70 meters showed a growth ring similar to those in Plate 20, Figure 70. The bordered pits are circular and the same arrangement as those figured in Text Figure 1, a, and b. Slide No. 15505, Museum of Paleontology, University of Michigan.

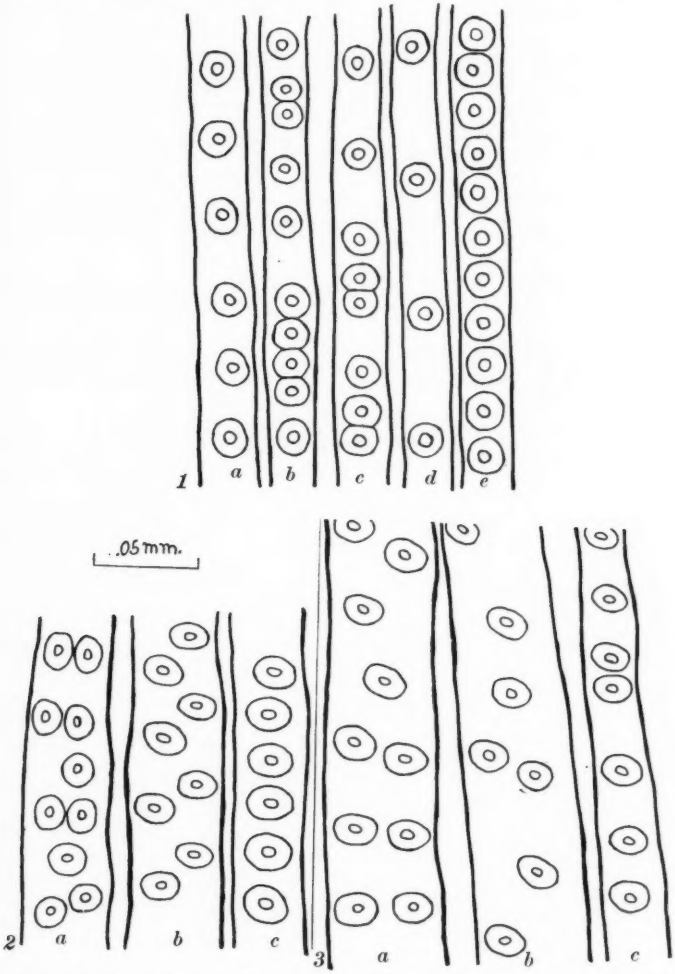
Circular and separate bordered pits, as well as a few contiguous ones such as those illustrated in Text Figure 1, were observed in a small piece of charcoal found in the coal sample collected at Evinasugsuit. Slide No. 15506, Museum of Paleontology, University of Michigan.

In the coal from Amisut, some specimens of charcoal showed uniseriate, oval bordered pits (Text Figures 1, c, and 2, c.), whereas the pitting in other specimens was circular and separate or contiguous (Text Figure 1). Slides No. 15507, 15508, Museum of Paleontology, University of Michigan.

The carbonized wood from Skansen, one-quarter of a mile west in a stream bed, at an altitude of about 15 meters, showed bordered pits that were slightly more oval than those illustrated in Text Figures 2, c, and 3, c. Circular bordered pits similar to those in Text Figure 1, a, b, e, were also observed in this material. No bars of Sanio were observed on any of the tracheids. Slide No. 15509, Museum of Paleontology, University of Michigan.

Both the abietineous and araucarian types of tracheary pitting occur in

Mesozoic conifers. In the former the bordered pits are more or less widely placed and when in more than one vertical row they are opposite each other, but in the latter type the bordered pits are contiguous and flattened and, when in more than one vertical series, alternate.



Figs. 1-3. *Cedroxylon* spp. These drawings illustrate the arrangement of the bordered pits that occur on the tracheids of the various specimens of charcoal.

The presence or absence of the so-called "rims" or "bars" of Sanio has been regarded by some paleobotanists as the most reliable diagnostic character in distinguishing woods of abietineous and araucarian affinities. The absence of these structures has been taken to indicate araucarian affinity, but Bailey (1933) has shown that they should not be relied upon entirely in the identification of fossil woods.

Fragments of carbonized wood or actual charcoal, the so-called mother of coal, occurred in almost every sample of coal examined. Nearly all the specimens observed, appeared to have been charred before burial in the original peat deposits. Such portions of the coals as had obviously been derived from woody material, always dissolved out completely during the process of maceration. The charcoal, on the contrary, was insoluble and always retained its structure. It seems certain therefore that the carbonized wood was charred by forest fires contemporary with the deposition of the beds, and that it was originally deposited as charcoal and not as wood.

ANGIOSPERMAE

Phyllodermium gen. nov.

Isolated cuticles or epidermal fragments, epidermal cells variously shaped; subsidiary cells specialized or sometimes not differentiated from adjacent epidermal cells; stomata scattered, not definitely oriented.

Phyllodermium Reinschii sp. nov.

Stomata irregularly scattered with no definite orientation; guard cells allantoid, 12-14μ wide, 35-50μ long; guard cells thickened in an elliptical rim around the stomatal opening; lateral and polar subsidiary cells not specialized in shape or size, slightly smaller than surrounding epidermal cells; epidermal cells polygonal, cell walls straight and smooth. Amisut, east coast of Disko Island, Greenland; Upper Cretaceous. Plate 21, Figures 72 and 73; Text Figure 5. Cotype. Slide No. 15486, Museum of Paleontology, University of Michigan.

Phyllodermium nervosum sp. nov.

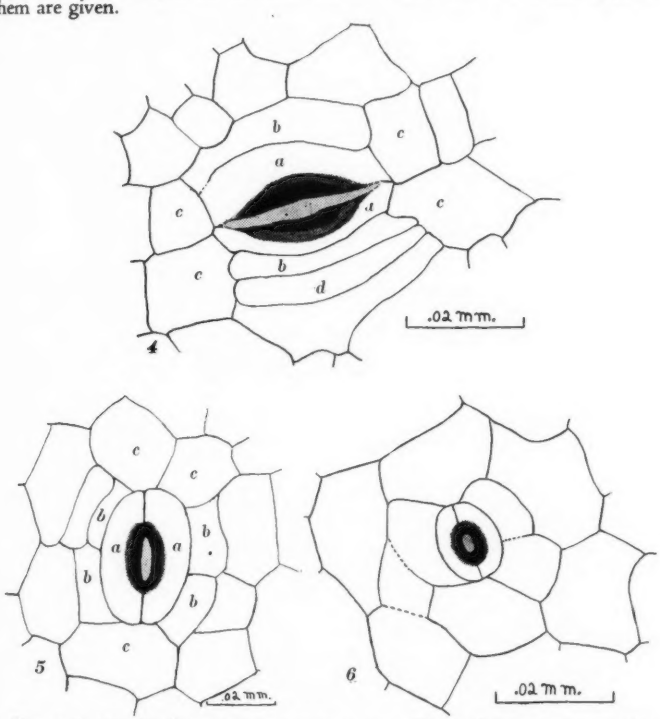
Stomata scattered with no definite orientation; guard cells 7-10μ wide, 15-33μ long; thickenings of guard cells somewhat lunate or seen in spindle-shaped pairs; lateral subsidiary cells narrow, oblong, as long as or longer than guard cells, one of two similar encircling cells present; polar subsidiary cells apparently not differentiated from surrounding epidermal cells; epidermal cells variously shaped, but mostly rectangular to square; cell walls straight and smooth. Skansen, east coast of Disko Island, Greenland; two miles inland at an altitude of 140 meters; Upper Cretaceous. Plate 21, Figures 74 and 75; Text Figure 4. Holotype. Slide No. 15482, Museum of Paleontology, University of Michigan.

Phyllodermium perplexum sp. nov.

Stomata scattered with no definite orientation; guard cells allantoid, 3.5-

7μ wide, 7-15μ long; guard cell thickenings nearly semicircular; lateral and polar subsidiary cells smaller than adjacent epidermal cells, otherwise not differentiated; epidermal cells polygonal to square, cell walls straight and smooth. Skansen, east coast of Disko Island, Greenland; two miles inland at an altitude of 140 meters; Upper Cretaceous. Plate 20, Figure 62; Plate 21, Figures 76 and 77; Text Figure 6. Cotype. Slide No. 15483, Museum of Paleontology, University of Michigan.

In the literature the terminology applied to the cells surrounding the stomata varies considerably. The specialized epidermal cells next to the guard cells are variously called accessory, auxiliary, subsidiary, supporting, or girdling cells. Florin (1931) recently revised the terminology applied to these cells and called the cells bordering the guard cells, subsidiary cells; and any specialized cells around the subsidiary cells encircling cells. In Text Figures 4 and 5 the arrangement of these cells is shown and the terms applied to them are given.



Figs. 4-6. (4) *Phyllodermium nervosum* sp. nov. (5) *P. Reinschii* sp. nov. (6) *P. perplexum* sp. nov. In (4) and (5) the cells adjoining the stomata are indicated; a, guard cells; b, lateral subsidiary cells; c, polar subsidiary cells; d, encircling cell.

The importance of epidermal characters as indicators of phylogenetic relationship has been discussed in considerable detail by Thomas (1930), Bandulska (1930-31, 1931), Florin (1931), Harris (1926, 1932), and others. With the exception of Bandulska, they were dealing almost entirely with gymnosperms. They find that in both recent and fossil plants cuticle characters are of diagnostic value. The work of Odell (1932) shows that any character of the epidermis of the vegetative organs of living angiosperms is unsatisfactory for diagnostic work. The epidermal characters of living angiosperms do not insure accurate specific or generic diagnosis, and this no doubt holds true also for fossil angiosperms.

Types of Cuticles

Epidermal or cuticular remains were found in almost every sample examined, but were much more abundant in some samples than in others. Cuticles without stomata or other characteristic features were more numerous and common than those with such characters. The most common cuticles without stomata and other similar tissues met with in this study will be designated as unnamed types, because of the lack of definite diagnostic features.

Type A.—This cuticle has the stomata arranged in rows, but the guard cells have disappeared leaving only a cavity. The other epidermal cells are long and narrow. The stomata do not appear to be definitely orientated, but otherwise this specimen is similar to the type of cuticle found in some of the Coniferae. Plate 20, Figure 62. Slide No. 15487, Museum of Paleontology, University of Michigan.

Type B.—The cells of this cuticle are mostly rectangular or square. The cell walls are very sinuous, and are of the type very common to many of the gymnosperms. Plate 22, Figure 78. Slide No. 15483, Museum of Paleontology, University of Michigan.

Type C.—The cells are rectangular or square but larger than those of Type B. The cell walls are sinuous but less so than in the preceding specimen. Cells of this type are also found in many gymnosperms. Plate 22, Figure 79. Slide No. 15483, Museum of Paleontology, University of Michigan.

Type D.—This is a rather thin cuticle with narrow hexagonal or somewhat rectangular cells. Plate 22, Figure 80. Slide No. 15492, Museum of Paleontology, University of Michigan.

Type E.—A rather thin cuticle with short, broad, rectangular or square cells. Plate 22, Figure 81. Slide No. 15849, Museum of Paleontology, University of Michigan.

Type F.—A thin cuticle with hexagonal cells. This type and types D and E were perhaps the most frequently observed cuticles. Plate 22, Figure 82. Slide No. 15488, Museum of Paleontology, University of Michigan.

Type G.—A thick cuticle with polygonal cells. This type is similar to type F in cell size and shape, but differs mostly in the greater thickness of

the cell walls. Plate 22, Figure 83. Slide No. 15491, Museum of Paleontology, University of Michigan.

Type H.—A thick specimen with small rectangular or square cells arranged more or less in definite rows. This appears to be more like cork tissue than epidermis. Plate 22, Figure 84. Slide No. 15490, Museum of Paleontology, University of Michigan.

The distribution of the types of epidermal or similar tissues is given in Table I.

Harris (1926, 1931) found that oxidative maceration followed by an alkali destroys the cuticles of ferns but not those of gymnosperms or of angiosperms. Since that type of maceration was used to soften the coal, perhaps most of the cuticles figured belong to the latter groups.

Plantae Incertae Sedis

Spermatites gen. nov.

Small, hollow structures varying considerably in size and shape, oblong-elliptical, ovate, oval, obovate, orbicular, or phaseoloid; wall cells small, square, hexagonal or rectangular; orifice small, apical or slightly lateral; base a dense mass of compact cells, sessile or short stalked. Plate 18, Figures 26-28; Plate 19, Figures 29-55; Plate 20, Figures 56-60. These very interesting little fossils rank next to *Selaginellites* (Miner, 1932), as the predominating type recovered from this coal. As to the exact affinities of these forms nothing definite can be said. Arnold (1932) wrote of them as "structures simulating bryophytic antheridia," but there is nothing exactly comparable to them among the present day Bryophyta. Superficially they somewhat resemble the perianth of *Sphaerocarpus*, but upon a closer examination, these organs appear quite different in structure. The possibility of their being sporangia was considered, but if so, one would expect to find at least a few spores associated with them, but spores were not found. Perhaps these fossils represent primitive orthotropous or slightly amphitropous seeds in which the orifice represents the micropylar opening and the dense basal portion the chalaza. The generic name *Spermatites* is employed as a convenient designation for such unassigned organs. Characteristic differences in size and shape must suffice to distinguish between species.

Spermatites elongatus sp. nov.

Oblong, or oblong-elliptical, apex obtuse; 298-448μ wide, 730-1080μ long, average 354 x 955μ; wall cells square to rectangular, 15-30μ wide, 30-75μ long; orifice apical. Skansen, east coast of Disko Island, Greenland; two miles inland at altitude of 140 meters; Upper Cretaceous. Plate 19, Figures 30-36, 38. Skansen, east coast of Disko Island, Greenland; two miles inland at an altitude of 385 meters; Upper Cretaceous. Plate 19, Figures 29, 37. This species is distinguished by its parallel or nearly parallel sides, and in being several times longer than wide. It is nearly uniform in width throughout the greater part of its length. The apex is obtuse and the pore is ter-

minal. The character of the small cells around the pore was rather difficult to determine. This species was perhaps the most abundant of this type of fossil. Cotypes. Slides No. 15468, 15469, 15471, 15474, 15475, 15479, 15480, 15481, Museum of Paleontology, University of Michigan.

Spermatites orbicularis sp. nov.

Orbicular or nearly so, 698-714μ wide, 730-865μ long, average size being about 720 x 780μ; wall cells square, rectangular, or hexagonal, mostly hexagonal, 26-45μ wide, 37-60μ long; orifice apical. Patoot, southeast coast of Nugsuaks Peninsula, Greenland, at 165 meters; Upper Cretaceous. Plate 18, Figures 27, 28. Skansen, east coast of Disko Island, Greenland; 2 miles inland at altitude of 140 meters. Plate 18, Figure 26. This uncommon type is characterized by its circular or nearly circular shape. The wall is mostly composed of hexagonal cells. The pore is terminal but the structure of the surrounding cells could not be determined. Cotypes. Slides No. 15477, 15480, Museum of Paleontology, University of Michigan.

Spermatites arcuatus sp. nov.

Phaseoloid, 415-481μ wide, 697-863μ long, average size about 442 X 780μ; wall cells square, or rectangular, mostly rectangular, 20-40μ wide, 30-67μ long; orifice apical. Skansen, east coast of Disko Island, Greenland; 2 miles inland at an altitude of 140 meters; Upper Cretaceous. Plate 19, Figures 48-51. The distinguishing feature of this species is its shape, with one side rounded or convex and the other side nearly straight or concave. It is rarely over twice as long as broad, with its greatest breadth at the middle. Both ends are somewhat obtuse, and the pore is apical. This species was not as common as *S. elongatus* but more so than *S. orbicularis*. Cotypes. Slides No. 15468, 15472, 15475, Museum of Paleontology, University of Michigan.

Spermatites ovatus sp. nov.

Ovate, 365-432μ wide, 780-946μ long, average about 386-847μ; wall cells rectangular, 22-37μ wide, 37-60μ long; orifice apical. Skansen, east coast of Disko Island, Greenland; 2 miles inland at an altitude of 149 meters; Upper Cretaceous. Plate 19, Figures 39, 40. This type is broadest just above the dense basal portion, and the sides taper gradually to an acuminate apex. The pore is terminal. This species was also rather uncommon, occurring about as frequently as *S. arcuatus*. Cotypes. Slides No. 15472, 15480, Museum of Paleontology, University of Michigan.

Spermatites nanus sp. nov.

Narrow elliptical, 266-315μ wide, 598-680μ long, average near 290 x 647μ; wall cells rectangular, 18-26μ wide, 30-45μ long; orifice apical. Skansen, east coast of Disko Island, Greenland; 2 miles inland at an altitude of 140 meters; Upper Cretaceous. Plate 19, Figures 52, 54. Skansen, east coast of Disko Island, Greenland; 2 miles inland at altitude of 385 meters; Upper Cretaceous. Plate 19, Figure 53. Although usually over twice as long as

wide, it is easily distinguished from *S. elongatus* by its small size. The sides are slightly rounded and the greatest width is through the central portion. The pore is terminal just as in most of the other species. This species has proved to be rather uncommon. Cotypes. Slides No. 15479, 15481, Museum of Paleontology, University of Michigan.

Spermatites ellipticus sp. nov.

Obovate-elliptical, 382-580μ wide, 664-930μ long, average about 465 x 780μ, apex more or less rounded; wall cells rectangular, 26-37μ wide, 35-52μ long; orifice apical. Skansen, east coast of Disko Island, Greenland; 2 miles inland at altitudes of 140 meters and 385 meters; Upper Cretaceous. Plate 19, Figures 41, 43-47. Patoot, southeast coast of the Nugsuaks Peninsula, Greenland, at an altitude of 165 meters; Upper Cretaceous. Plate 19, Figure 42. This rather common species is characterized by being not over twice as long as wide, with usually rounded sides and apex, and its greatest width being at or slightly above the middle. This species is found as abundantly as *S. elongatus*. Cotypes. Slides No. 15470, 15473, 15476, 15477, 15478, 15480, Museum of Paleontology, University of Michigan.

Spermatites pylophorus sp. nov.

Obovate, oblong-elliptical, 315-531μ wide, 764-1029μ long, average being about 420 x 860μ; wall cells square to rectangular, 20-30μ wide, 26-52μ long; orifice lateral, near the apex. Skansen, east coast of Disko Island, Greenland; 2 miles inland at an altitude of 140 meters; Upper Cretaceous. Plate 19, Figure 55; Plate 20, Figures 56-60. This species varies a little more in size and shape than do the others in this form-genus. Its distinguishing feature is the lateral position of the orifice. The position of the orifice appears to be natural and not the result of any distortion. This type was about as abundant as *S. ellipticus*. Cotypes. Slides No. 15467, 15475, 15478, 15479, 15480, Museum of Paleontology, University of Michigan.

Carpolithus Linn.

Carpolithus patootensis sp. nov.

A small seed, ovate, plano-convex; 4 mm. wide, 6 mm. long, and 1 mm. thick; testa smooth; point of attachment apparently near the base on the plane side. Patoot, southeast coast of the Nugsuaks Peninsula, at an altitude of 165 meters; Upper Cretaceous. Plate 18, Figures 23-25. Only a single specimen of this small seed was found. It is rounded on the one side and more or less flattened on the other; widest at the middle and not much longer than wide. Holotype. No. 15459, Museum of Paleontology, University of Michigan.

Carpolithus amisutensis sp. nov.

A minute seed, ovate-elliptical, 1.4 mm. wide, 3 mm. long, about .5 mm. thick; testa rugose; no point of attachment discernible. Amisut, east coast of Disko Island, Greenland, at an altitude of 1 meter; Upper Cretaceous. Plate 18, Figure 21. Only a single specimen of this seed was found. It is just a little over twice as long as wide, with the greatest width near the mid-

dle. The sides are slightly rounded and wavy in outline, due to the wrinkled nature of the seed coat. In the type specimen part of the seed coat has been broken away. Holotype. No. 15458, Museum of Paleontology, University of Michigan.

Alatampulla gen. nov.

Small winged seeds, longer than broad; wing rather uniform in width, completely surrounding the nucula or nucular cavity. This genus differs from *Samaropsis* in that in the latter genus are included seeds of the samaroid type which are approximately circular, and much larger.

Alatampulla Bartlettii sp. nov.

Winged seeds, elliptical, .6-1.1 mm. wide, 1.3-2.3 mm. long; wing .1 mm. in width, slightly narrower at the apex and wider at the base; nucular cavity vase-shaped, .4-.6 mm. wide, 1-1.6 mm. long; surface smooth. Amisut, east coast of Disko Island, Greenland; Upper Cretaceous. Plate 18, Figure 20, Skansen, east coast of Disko Island, Greenland; 2 miles inland at an altitude of 140 meters. Three specimens of this very interesting little winged seed were found. Cotype. Slide No. 15457, Museum of Paleontology, University of Michigan.

FOSSILIS INCERTAE SEDIS

Arcellites gen. nov.

Body small, circular with few to several short tube-like appendages, surface pitted, pits minute.

Arcellites disciformis sp. nov.

Rotund, 265-350μ in diameter, the average being 310μ; surface pitted; 12-24 tube-like appendages, 24-30μ in width and 35-88μ in length, with sides usually parallel, or sometimes slightly constricted near the base; orifices of appendages broadly elliptical, averaging about 10 X 14μ in diameter. Skansen, east coast of Disko Island, Greenland; 2 miles inland at an altitude of 140 meters; Upper Cretaceous. Plate 20, Figures 61, 64-66. This fossil resembles somewhat a flattened exine of a megaspore, but the arrangement and structure of the tube-like appendages seems to indicate that it is the chitinous shell or covering of some small unicellular animal rather than the remains of a plant. Some of the fresh water *Rhizopoda* have similar chitinous shells, such as those in the genus *Arcella*. While the species described above differs greatly in many important respects from present day fresh water *Rhizopoda*, it is not at all improbable that it could not be an extinct form of that group or of a closely related one. The tube-like appendages are unknown in any of the living rhizopods, and no other special opening for a mouth could be detected in this species. The openings into the specimens appear to be through the appendages. The conditions necessary for the accumulation of peat are usually characteristic of the habitats of many of the fresh water rhizopods. Cotypes. Slides No. 15497, 15498, Museum of Paleontology, University of Michigan.

Table 1. Distribution of the fossils recovered from the Greenland Coal.

Species / Localities	Amisut (No other data)	Amisut At altitude of 1 meter.	Atanikerdluk At end of peninsula at sea level.	Evinasuguit along coast between Skansen and Godhavn.	Patoot At altitude of 85 meters.	Patoot At altitude of 165 meters.	Patoot At altitude between 200 and 300 meters.	Skansen 2 miles inland at altitude of 140 meters.	Skansen 2 miles inland at altitude of 385 meters.	Skansen 1 mile inland at altitude of 175 meters.	Skansen 1 quarter mile west in stream bed at 15 meters.	Skansen 1 and one-half miles west and 1 and one-half inland at altitude of 70 meters.
Selaginellites Arnoldii					+	+		+				
S. borealis						+		+				
S. Ariadnae								+				
S. inornatus								+				
S. echinatus								+				
S. greenlandicus								+				
S. Erlansonii								+				
S. papillosus								+				
S. subrotundus								+				
Chrysotheca diskoensis	+								+			
Thecopteris major									+	+		
T. minor												
Spermatites elongatus								+	+			
S. orbicularis						+		+				
S. arcuatus								+				
S. ovatus								+				
S. nanus								+	+			
S. ellipticus						+		+	+			
S. pylophorus								+				
Carpolithus patootensis						+						
C. amisutensis		+										
Alatampulla Bartlettii	+							+				
Phyllodermium Reinschii	+											
P. nervosum								+				
P. perplexum								+				
Arcellites disciformis								+				
Cuticles												
Type A.								+				
Type B.								+				
Type C.								+				
Type D.			+			+	+	+	+			
Type E.	+	+				+	+	+				
Type F.	+					+				+		
Type G.	+							+				
Type H.		+				+			+			
Bordered pits												
Type of Text Figure 1, a.	+			+				+			+	+
Type of Text Figure 1, b.								+				+
Type of Text Figure 1, c.	+			+				+				
Type of Text Figure 1, d.	+							+			+	
Type of Text Figure 1, e.				+				+			+	
Type of Text Figure 2, a.									+			
Type of Text Figure 2, b.									+			
Type of Text Figure 2, c.	+								+		+	
Type of Text Figure 3, a.									+			
Type of Text Figure 3, b.									+			
Type of Text Figure 3, c.									+		+	

Climate

The question as to the nature of the climate during any geological interval is always interesting and offers opportunity for speculative thought. This is especially true when fossil forms are found in the Arctic regions, the only living representatives of which are at the present time restricted to the equatorial zone.

The presence of apparently tropical species in the rocks as far north as Greenland has led to the belief that a tropical or subtropical climate once existed in that northern country. To account for this various explanations and theories have been advanced, such as the wandering of the poles or the sliding movement of the earth's crust, all of which would seem to have been unnecessary if the fossil flora had been considered or known in its entirety. There is of course no doubt that the climate in Western Greenland was warmer during the Cretaceous time than at present, just as the climate of the Great Lakes and adjacent regions is warmer today than during the Pleistocene glaciation. Since environments in the world have changed during the course of time, the plants themselves have all probably changed in their reactions to external conditions.

Seward (1927) and Berry (1930) have recently questioned the existence of a tropical climate in this northern country during the late Mesozoic. They think that the flora thrived there under much more temperate conditions than has been assumed before. This assumption is supported from the present study of the Cretaceous coals of Western Greenland.

There can be little doubt that the plants which contributed to these coal beds did grow within the Arctic region, and that the coal is autochthonous in origin. There has never been any substantial evidence that coal is of allochthonous origin. Coal is metamorphosed peat and one of the conditions necessary for the favorable formation of peat is a cool to moderate climate. Peat forms in Arctic regions at the present time just as it did in past geological ages. It is much more extensive in Arctic regions than in the tropics as conditions in the latter are unfavorable for the accumulation of large or good peat deposits.

Growth rings occur in woods which grow in regions where there are periods of suspension in the activity of growth. This interruption of growth may be due to drought or to the lowering of the temperature. In general, then, growth rings indicate seasonal changes in a climate. Antevs (1925) states that growth rings are most marked in temperate zones and the distinctness increases with the latitude until climatic conditions exert a checking influence on their development. In Arctic regions growth rings are often indistinct and sometimes difficult to discern, while in the tropics they vary from distinct ones to those that are indiscernible or lacking. The lack of growth rings is an exception in temperate regions.

The growth rings in the pieces of coniferous charcoal are clearly defined. In their general nature and breadth, they are similar to those that occur in most coniferous trees growing today in temperate climates. A transverse section of a piece of charcoal from Skansen, 2 miles inland at an altitude of 140 meters is shown on Plate 20, Figure 67. The growth ring in this specimen is distinct, with a known breadth of about 3.2 mm. A cross section of another

specimen (Plate 20, Figure 70) from Skansen, 2 miles inland at an elevation of 385 meters, shows three lines of growth in a width of about 2 mm. but as this specimen is badly crushed its actual breadth would be slightly more than that given. Other specimens from the same locality, but not figured, show from one to three growth rings similar to those mentioned.

Discussion and Conclusion

The study of the coals of Western Greenland adds a new aspect to the fossil floras from that region. This new coal flora is based on the remains of plants that no doubt inhabited bogs or swamps. At present it is impossible to correlate the coal beds of Western Greenland with those of other regions because of the lack of information concerning the plant remains of other coals.

Not all of the coal studied can be correlated with each other as some of the coal samples did not yield sufficient or satisfactory plant remains. Definite correlations can be established between some of the coal deposits at Skansen and at Patoot.

Spermatites elongatus, S. ellipticus, and *S. nanus* occurred at Skansen, 2 miles inland at elevations of 140 and 385 meters. *S. ellipticus* also occurred at Patoot at an altitude of 165 meters, and *S. orbicularis* was found at the above locality as well as at Skansen, 2 miles inland at the altitude of 140 meters. *Selaginellites Arnoldii* and *S. borealis* both occurred at Skansen, 2 miles inland at an elevation of 140 meters and at Patoot at an altitude of 165 meters, but in addition *S. Arnoldii* was found at Patoot at a height of 85 meters. The distribution of the above mentioned species probably shows that the coal beds in which they occurred are closely correlated. It correlates beds at Skansen, Disko Island, 2 miles inland at heights of 140 and 385 meters, with those at Patoot, Nugsuaks Peninsula, at altitudes of 85 and 165 meters.

The distribution of this coal flora is summarized in Table I. The occurrence at different horizons of some of the same types of plant fragments, such as cuticles and carbonized wood, indicates also that these beds must have been formed by the same species or closely related ones.

The modern groups presumably represented by this flora are the Bryophyta, Pteridophyta and Spermatophyta. The Bryophyta are doubtfully represented by one species of *Chrysotheca;* the Pteridophyta by nine species of *Selaginellites,* and two species of *Thecopteris;* the Spermatophyta by representatives of the Gymnospermae and Angiospermae. The former are represented by three types of cuticles which may belong to the Coniferae, and by *Cedroxylon* spp. as indicated by the various fragments of carbonized wood. The Angiospermae present belong to the Dicotyledoneae, as is shown by the three species of *Phyllodermium.* The other types of cuticles apparently belong to the angiosperms. There are ten species of plants of uncertain affinities classified as follows: seven species of *Spermatites,* two species of *Carpolithus,* and one species of *Alatampulla.* A fossil of altogether uncertain position, *Arcellites,* is also present. It is probably an animal.

The present paper opens up a new field in the paleobotanical study of Mesozoic and Tertiary coals. Needless to say, much more must be done be-

fore extensive correlations of coals on the basis of botanical composition become possible. The characteristic and readily diagnosed fossils, however, give every reason to believe that the investigations will become cumulatively important as they are carried farther. It is the writer's intention to continue his studies which were begun here.

Summary

1. The fossils described in this study are all new, and they add a new phase to the paleobotanical and geological history of the fossil floras from Western Greenland.

2. Nine different genera are discussed, six of which are new; twenty-six species are discussed.

3. Eight types of cuticles or similar tissues that represent the most abundant ones recovered from this coal are discussed. Three of these types apparently belong to the gymnosperms, and the other five types belong to the angiosperms.

4. All the carbonized wood is coniferous. The tracheid pitting is abietineous in character.

5. Correlations are established between some of the coal beds at Patoot and Skansen.

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PLATE 18

(The numbers given are the catalogue numbers of the Museum of Paleontology, University of Michigan).

FIGURES

1–10. *Chrysotheca diskoensis*. x30. Cotypes. Slides No. 15455, 15456.

11–15. *Thecopteris major*. Figures 11 and 12 show the sporangia with the annuli partly surrounding the central mass of spores. x55. Figure 13, a circular mass of spores. x55. Figures 14 and 15, the characteristic spores. x340. Cotypes. Slides No. 15460-15463.

16–19. *Thecopteris minor*. Figure 16 shows the general shape of the sporangium. x55. Figure 17, a mass of spores. x55. Figures 18 and 19, the characteristic spores. x340. Cotypes. Slides No. 15460, 15462, 15464.

20. *Alatampulla Bartlettii*. x15. Cotype. Slide No. 15457.

21. *Carpolithus amisutensis*. x11.6. Holotype. Slide No. 15458.

22. *Selaginellites Arnoldii*. x90. No. 15466.

23–25. *Carpolithus patootensis*. Three different views of the same specimen. x5. Holotype. No. 15459.

26-28. *Spermatites orbicularis*. x30. Cotypes. Slides No. 15477, 15480.

PLATE 18

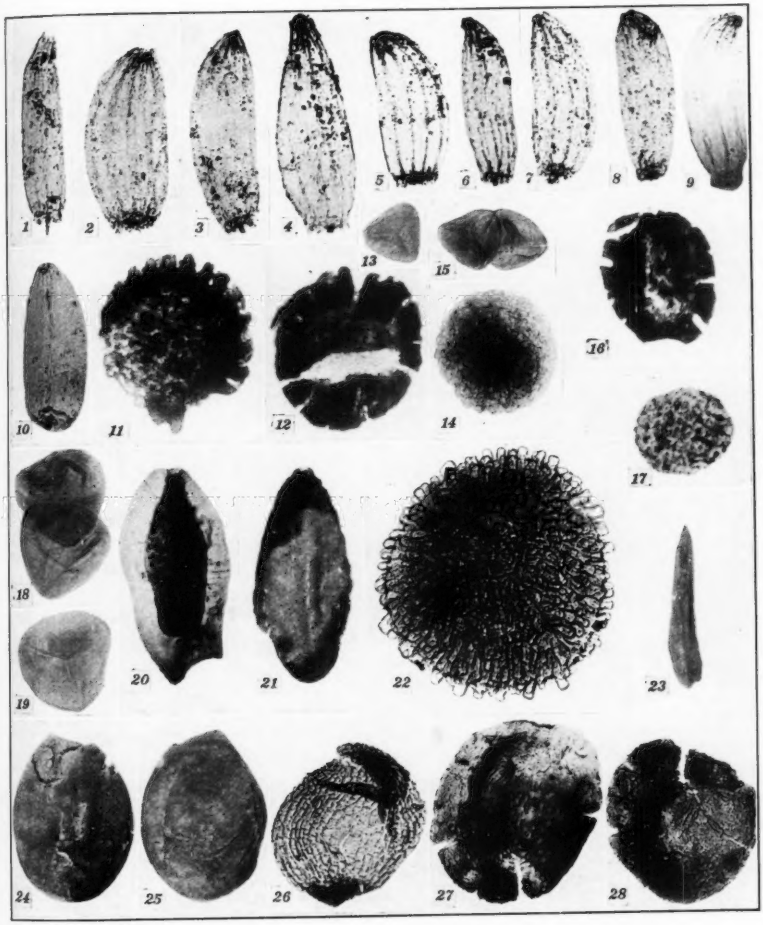

PLATE 19

FIGURES

29–38. *Spermatites elongatus.* x30. Cotypes. Slides No. 15468, 15469, 15471, 15474, 15475, 15479-15481.

39–40. *Spermatites ovatus.* x30. Cotypes. Slides No. 15472, 15480.

41–47. *Spermatites ellipticus.* x30. Cotypes. Slides No. 15470, 15473, 15476-15478, 15480.

48–51. *Spermatites arcuatus.* x30. Cotypes. Slides No. 15468, 15472, 15478.

52-54. *Spermatites nanus.* x30. Cotypes. Slides No. 15479, 15481.

55. *Spermatites pylophorus.* x30. Cotype. Slide No. 15480.

PLATE 19

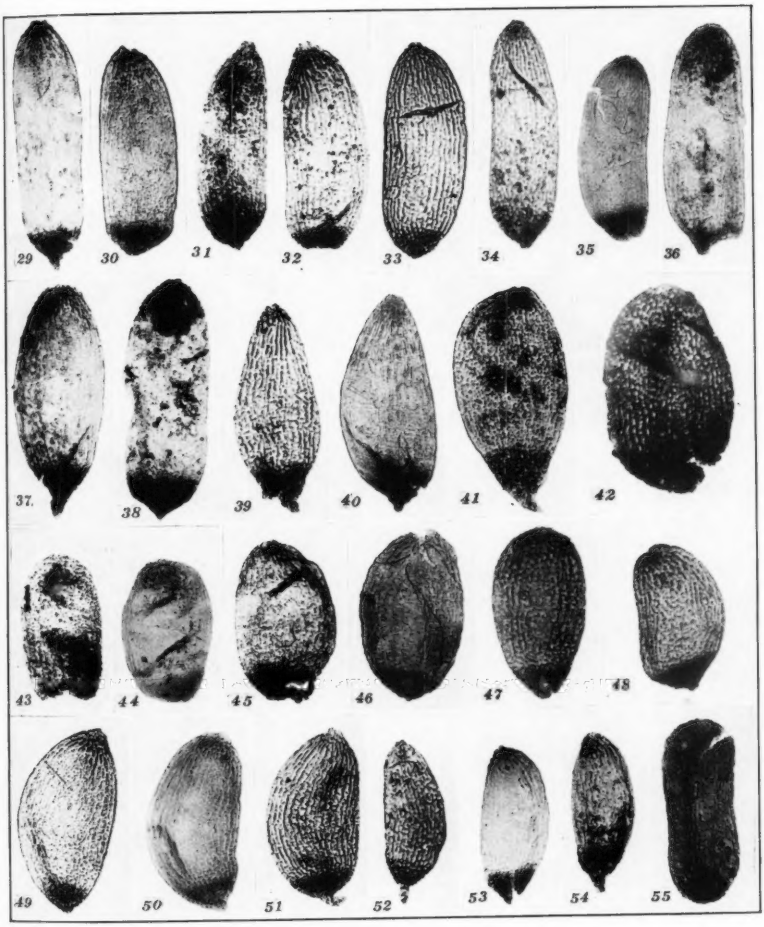
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PLATE 20

FIGURES

56–60. *Spermatites pylophorus.* x30. Cotypes. Slides No. 15467, 15475, 15478, 15480.

61. *Arcellites disciformis.* x100. Cotype. Slide No. 15497.

62. *Phyllodermium perplexum.* x95. Cotype. Slide No. 15483.

63. Cuticle Type A. x95. Slide No. 15487.

64–66. *Arcellites disciformis.* x100. Cotypes. Slides No. 15497, 15498.

67–69. Transverse and radial sections from a piece of charcoal. Figure 67 shows one growth ring. x15. Figure 68, an enlargement of a portion of the growth ring shown in Figure 67. x130. Figure 69, a radial section showing a part of a ray and the bordered pits on the tracheids. x130. Slide No. 15502.

70–71. Transverse section of a piece of charcoal showing three distinct growth rings. x15. Figure 71, an enlarged portion of Figure 70. x130. Slide No. 15503.

PLATE 20

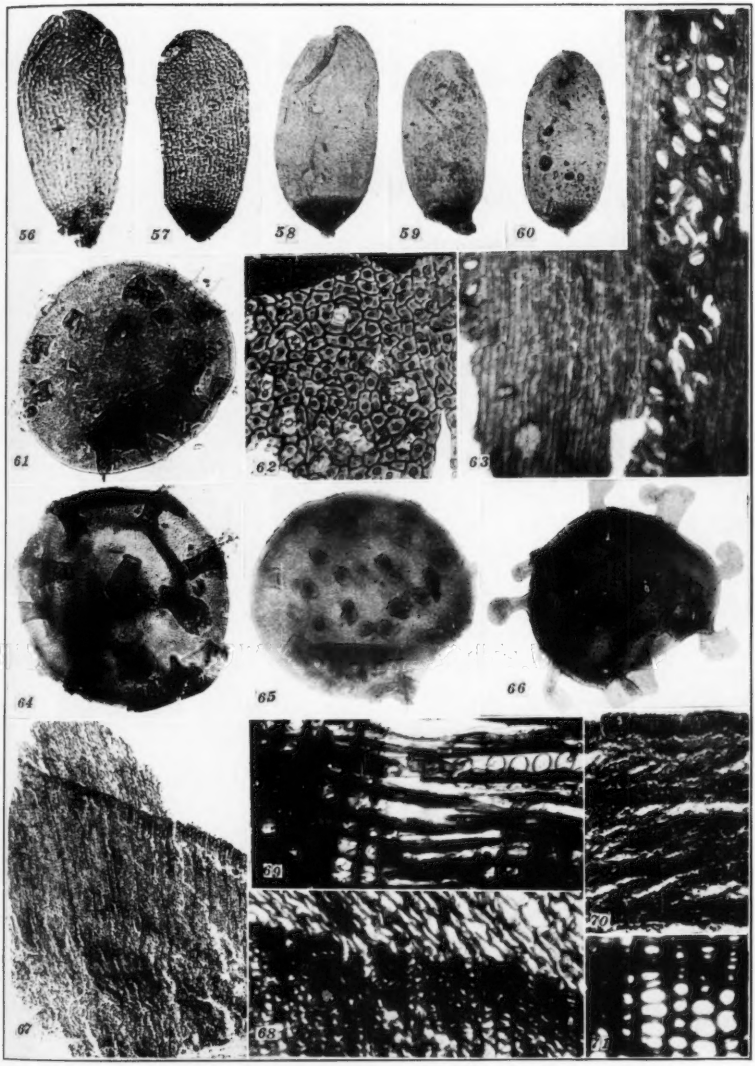


PLATE 21

FIGURES

72–73. *Phyllodermium Reinschii.* Figure 72, general arrangement of stomata. x95. Figure 73, an enlargement of a portion of Figure 72. x340. Cotype. Slide No. 15486.

74–75. *Phyllodermium nervosum.* Figure 74, the general arrangement of the stomata. x95. Figure 75, an enlargement of a portion of Figure 74. x340. Holotype. Slide No. 15482.

76–77. *Phyllodermium perplexum.* Figure 76 shows the distribution of the stomata. x95. Figure 77, an enlargement of a portion of Figure 76. x340. Cotype. Slide No. 15483.

PLATE 21

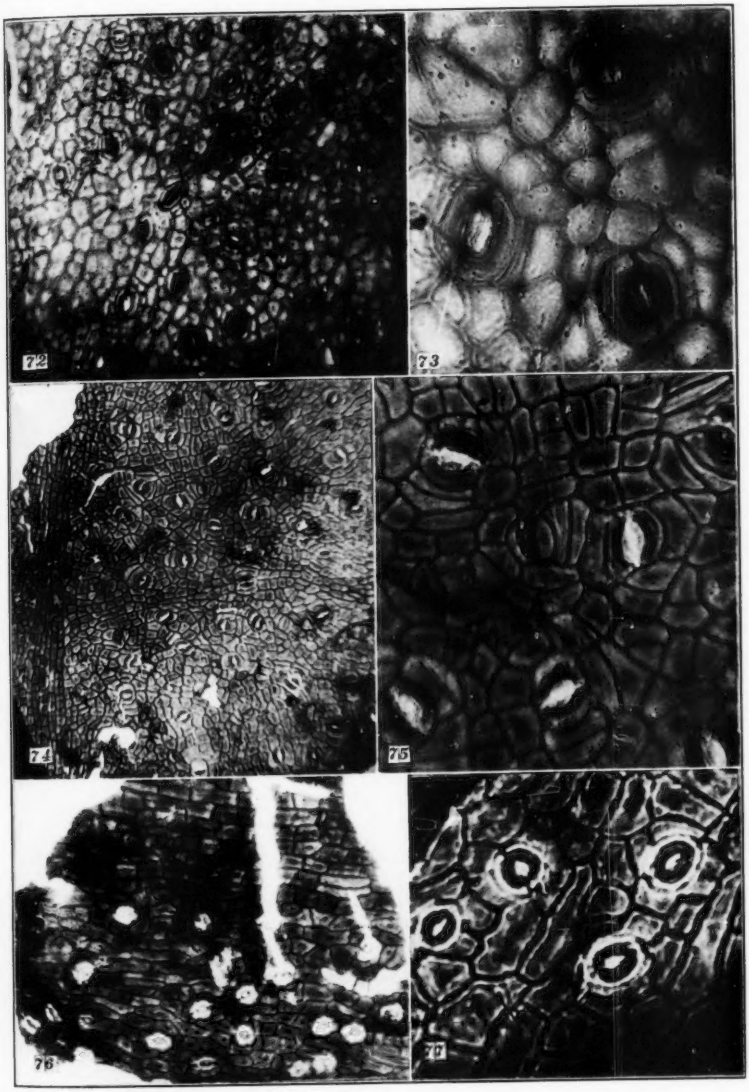


PLATE 22

FIGURES

78. Cuticle Type B. x95. Slide No. 15483.

79. Cuticle Type C. x95. Slide No. 15483.

80. Cuticle Type D. x95. Slide No. 15492.

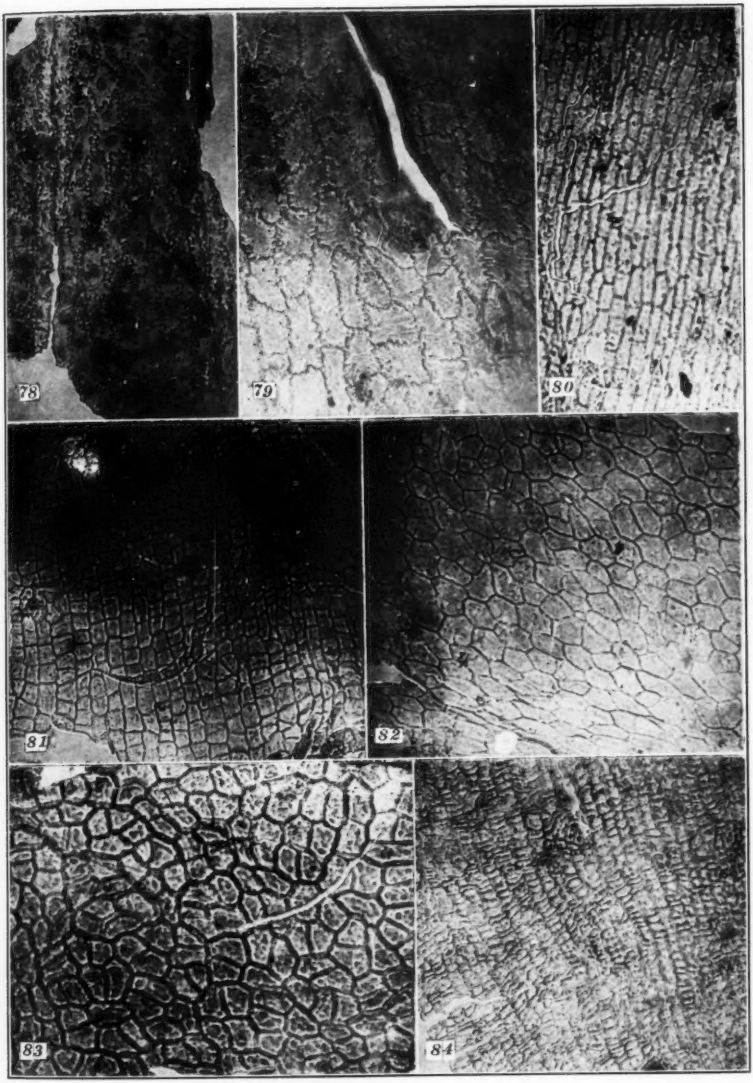
81. Cuticle Type E. x95. Slide No. 15489.

82. Cuticle Type F. x95. Slide No. 15488.

83. Cuticle Type G. x95. Slide No. 15491.

84. Cuticle or cellular tissue Type H. x95. Slide No. 15490.

PLATE 22



II. CRETACEOUS AND TERTIARY COALS FROM MONTANA*

The plant fossils studied in this report were recovered from coal which came from Cascade and Carbon counties, Montana. The Cascade County sample was collected by Dr. Louis Hall of Ann Arbor, and given by him to Professor H. H. Bartlett who turned the material over to the writer. The Carbon County sample was secured from Mr. W. H. Homer, operator of the Homer Coal Mining Company at Bear Creek, Montana. Coal vein No. 4.

The coal deposits of Cascade County are in the Great Falls coal field (Barrett, 1916; Fisher, 1907) and throughout this field the coal occurs in the lower part of the Kootenai formation, which is of Lower Cretaceous age (Fisher, 1909).

In Carbon County the coal beds belong to the Bear Creek coal field (Fisher, 1906) or to the Red Lodge coal field (Woodruff, 1909). The same coal seams occur in both the Bear Creek and Red Lodge districts. The exact formation in which the coal beds of this field belong appears to have been rather difficult to determine. Fisher (1906) stated that the coal of Bear Creek district occurs in the upper part of the so-called Laramie formation, but the later works of Darton (1907), Woodruff (1909), and Calvert (1916) all agree in placing it in the Fort Union formation, which they considered as belonging to the lower portion of the Tertitary. Darton (1907) in commenting upon the Cretaceous system in this basin states that the upper limits could not be ascertained and that probably a large part of the upper beds, as well as the Red Lodge-Bear Creek coal bearing rocks are of early Eocene or Fort Union age.

For many years there has been considerable controversy over the stratigraphic position of the Fort Union formation. The data available concerning the position or age of this formation has been interpreted in various ways by different paleontologists; some have placed it at the top of the Cretaceous, but others have put it at the base of the Tertiary.

In many localities the Fort Union formation lies immediately above the Cannonball member of the Lance formation, and Stanton (1920) after making a study of the fauna of the Cannonball member concluded that it and consequently the whole of the Lance formation is of Cretaceous age. All of the evidence does not allow for the existence of a long unrepresented interval any-where between the Fox Hills and Wasatch formations. From the faunal evidence as given by Stanton, Schuchert (1921, 1922) concluded that the division between the Mesozoic and Cenozoic apparently lies between the Fort Union and Wasatch formations and not the Fox Hills and Lance beds.

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* Papers from the Department of Botany and Herbarium of the University of Michigan, No. 460.

Miller (1928) also places the Fort Union at the top of the Upper Cretaceous as Schuchert (1924) still maintains that it should be.

The works and opinions of such investigators as Cross (1921, 1922), Knowlton (1921, 1922), Simpson (1929), Scott (1932), Jepsen (1930), Russell (1930), Schuchert and Dunbar (1933), and others, indicate that Fort Union belongs to the Tertiary. Knowlton (1921, 1922) states that the Fort Union flora is typically Eocene in age and that there is a floral continuity between the Lance and the overlying beds of the Fort Union. Therefore the two formations should not be separated but considered as being of the same age. The paleozoological evidence does not support the paleobotanical view given by Knowlton. Simpson (1929) from his study of the Fort Union mammalian fauna at Bear Creek, Montana, places the Lance formation at the summit of the Upper Cretaceous and the Fort Union in the Paleocene, which is the oldest of the Tertiary series. Scott (1932) likewise considers the Fort Union as being in the Paleocene. In their latest work Schuchert and Dunbar (1933) state that the faunal evidence now appears to be conclusive that the Fort Union formation belongs to the Cenozoic. Beds identified as Fort Union show a definite correlation with the oldest Cenozoic or Paleocene formations. The Lance formation with its dinosaurs is clearly the latest interval of the Cretaceous.

This report presents a few characteristic plant fossils recovered from coal belonging to the Kootenai and Fort Union formations. It is hoped that as more work of this nature is done, these fossils will prove to be of more stratigraphic importance.

During the course of this study about 45 samples of coal were examined. The samples were secured from the coal fields of Montana, Wyoming, Colorado, Utah, and New Mexico; but, as yet, no recognizable fossils have been found in the other samples.

The cotypes are in the collections of Ernest L. Miner and the Museum of Paleontology, University of Michigan. The numbers given are the catalogue numbers of the Museum.

The coal was macerated in bulk and the larger isolated plant fragments, with the exception of the charcoal were mounted on slides in euparal (Miner, 1932).

"Smear" mounts (Miner, 1935) were made of the finer plant remains that were too small to be recovered with a binocular microscope.

The charcoal was embedded in paraffin by the butyl alcohol method, and then cut into serial sections on a rotary microtome. The sections were mounted on slides without removing the paraffin because if the paraffin were removed the charcoal would crumble to pieces. Euparal was used as the mounting medium.

The plant remains from the Cascade coal consisted mostly of cuticles and a few spores. The Carbon County sample contained some very interesting and characteristic megaspores, a few pieces of fairly well preserved charcoal.

and some cuticles. The plant remains in the Cascade coal appeared to have undergone more distintegration than those in the other sample.

Selaginellites mirabilis sp. nov.

Plate 23, Figs. 1-6.

Body of exine round, 332-498μ in diameter, the average being 395μ; exine covered with irregular reticulate ridges which extend up part way on the wings; triradiate markings extend beyond the periphery; diameter on the radii of the triradiate markings 430-630μ; triradiate markings winged, wings 67-150μ in width, the average width being about 90μ; equatorial ring present. Bear Creek, Carbon County, Montana; Fort Union formation. Cotypes. Slides No. 15510, 15511, 15512, Museum of Paleontology, University of Michigan. This beautiful megaspore is quite abundant and appears to be characteristic of the coal. The shape and appearance of this spore varies somewhat, depending upon the plane in which it was flattened. When compressed so that it can be viewed from the inner or outer faces it is triangular in shape (Figures 1-3), but when flattened laterally the rounded outer face can be seen with the wing of the triradiate markings extending up over the inner face and the equatorial ring separating the two faces (Figures 4-6).

The presence of the equatorial ring is quite interesting as it is present on megaspores of *Isoetes*, but it is not always present or evident on megaspores of *Selaginella*. For a more complete discussion of megaspores of this type the reader is referred to a previous article (Miner, 1932).

Deltoidospora gen. nov.

Small unassigned deltoid or sub-deltoid spores of the type that is commonly found associated with many Mesozoic ferns; such as *Gleichenites*, *Gleicheniopsis*, *Laccopteris*, and others.

Deltoidospora Hallii sp. nov.

Plate 24, Figs. 7-8.

Body of exine deltoid, 33-39μ in diameter; sides straight or slightly curved inwards; triradiate clefts extend two thirds or more of the distance to the periphery. Cascade County, Montana; Kootenai formation. Cotypes. Slides No. 15515, 15516, Museum of Paleontology, University of Michigan.

Deltoidospora cascadensis sp. nov.

Plate 24, Figs. 9-12

Body of exine sub-deltoid, 30-41μ in diameter; sides rounded; triradiate clefts extending two thirds or more of the distance to the periphery. Cascade County, Montana; Kootenai formation. Cotypes. Slides No. 15515, 15516, Museum of Paleontology, University of Michigan. This species somewhat resembles *Sporonites Neddeni* of Potonié (1931), from the Tertiary brown coal of Germany, but the great difference in the age makes it hardly seem possible to consider them as belonging to the same species. In the form-genus *Sporonites*, Potonié places a great variety of small unassigned spores.

The generic designation *Deltoidospora* as used here includes the isolated spore types that are common to many Mesozoic ferns.

Sporonites montanensis sp. nov.
Plate 24, Figs. 13-16.

Body of exine round or nearly so, 55-60μ in diameter; no triradiate clefts or other markings visible. Cascade County, Montana; Kootenai formation. Cotypes. Slides No. 15515, 15516, Museum of Paleontology, University of Michigan.

Cedroxylon sp.
Plate 24, Figs. 17-20.

In the sample of coal from Bear Creek, a piece of charcoal was discovered which in transverse section shows ten distinct growth rings. The charcoal was so badly crushed that not much detail, other than the arrangement of the bordered pits on the radial walls of the tracheids, could be observed.

The bordered pits are circular, and are arranged in one, two, or three vertical rows on the tracheids. The rows are opposite and the bordered pits are usually separate. A single tracheid sometimes has a combination of all three arrangements. Slide No. 15514, Museum of Paleontology, University of Michigan.

The medullary rays are narrow and have few to several pits per tracheid. The exact height and width of the rays could not be determined.

Distinct bars of Sanio are present on some of the tracheids but apparently absent from others.

The arrangement of the bordered pits on the radial walls of the tracheids and the pitting on the ray cells is very similar to that found in *Cedroxylon Nordenskjoldi* described by Mathiesen (1932) from some fossil wood collected at Turner Sound, East Greenland.

Among the genera for fossil coniferous woods this material can be placed in the form-genus *Cedroxylon* as defined by Bailey (1933).

The presence of the growth rings in this carbonized wood indicates that the climate, at the time the coal was deposited, was temperate. In order for such extensive coal deposits to accumulate during early Tertiary time, there must have been extensive aquatic and subaquatic habitats.

The plant remains recovered from these Montana coals are of similar types, i.e., spores, charcoal, cuticles, to those found in the coals from Western Greenland (Miner 1932, 1935), but the species represented are entirely different. *Selaginellites mirabilis*, which is the characteristic spore type found in the Bear Creek sample, is quite different from any of the species of the genus that were found in the coal from Skansen, Disko Island, and Patoot, Nugsuaks Peninsula, Western Greenland.

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DEPARTMENT OF BOTANY,
UNIVERSITY OF MICHIGAN,
ANN ARBOR, MICHIGAN.

PLATE 23

FIGURES

1–3. *Selaginellites mirabilis*. Spores compressed horizontally, so that they are triangular in shape.

4–6. *Selaginellites mirabilis*. Spores compressed laterally. x103. Cotypes. Slides No. 15510, 15511, 15512, Museum of Paleontology, University of Michigan.

PLATE 23

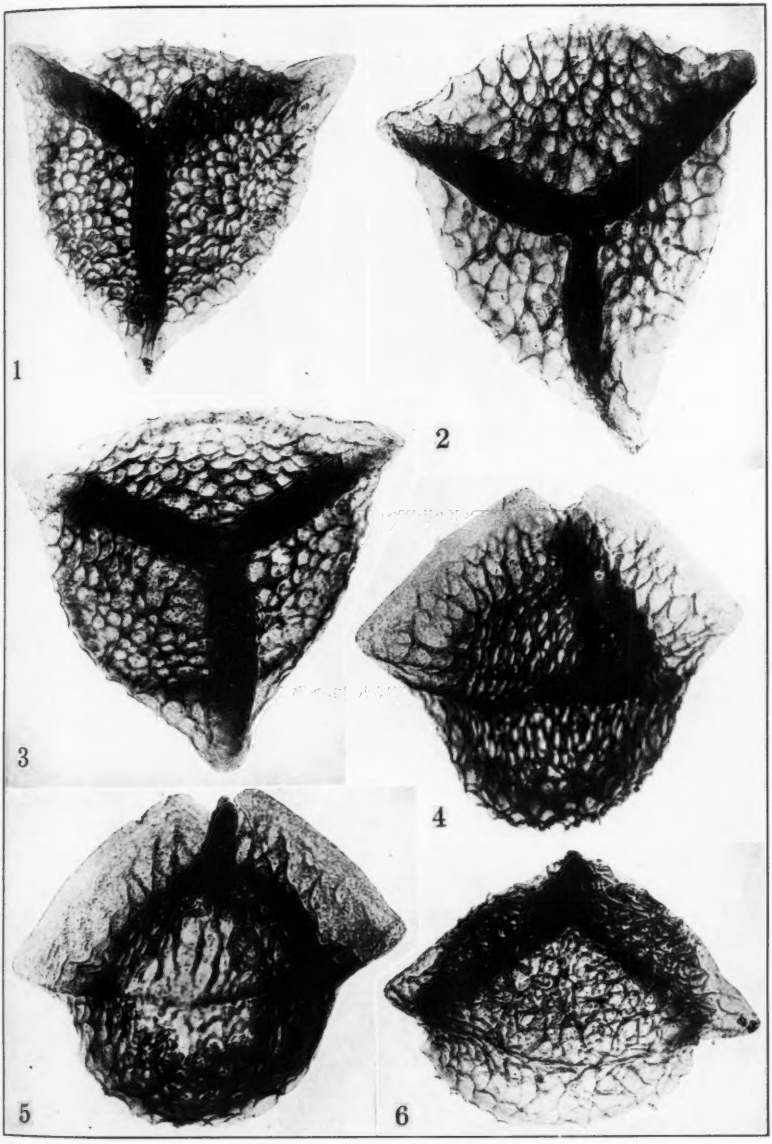


PLATE 24

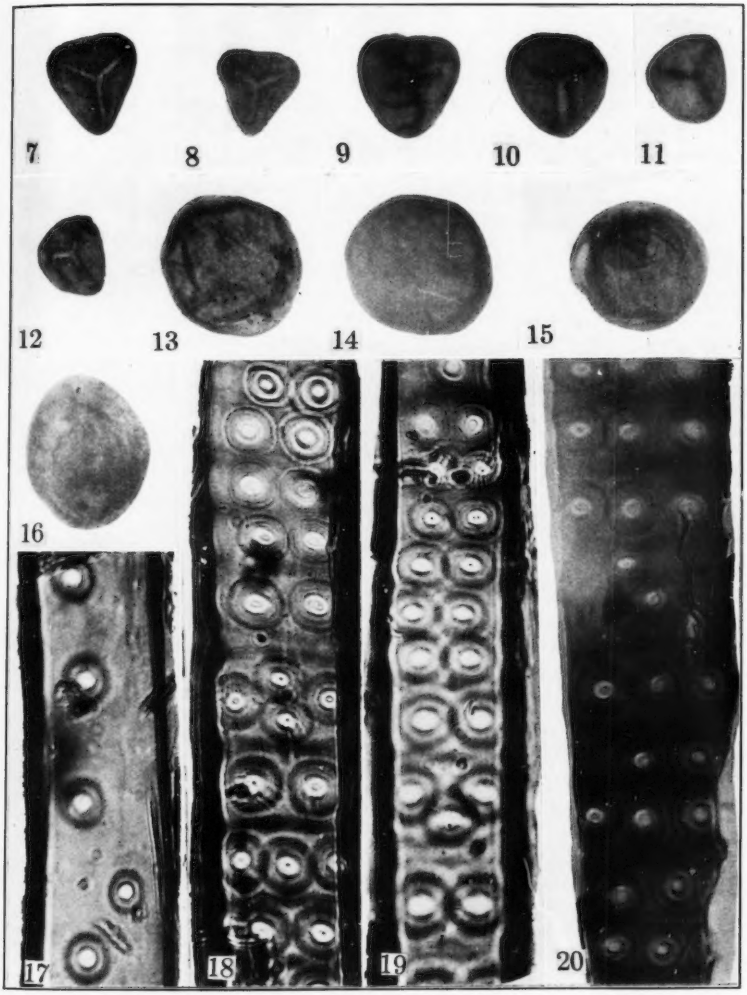
FIGURES

7–8. *Deltoidospora Hallii.* x340. Cotypes. Slides No. 15515, 15516, Museum of Paleontology, University of Michigan.

9–12. *Deltoidospora cascadensis.* x340. Cotypes. Slides No. 15515, 15516, Museum of Paleontology, University of Michigan.

17–20. Tracheids from the charcoal, showing the arrangement of the bordered pits. Bars of Sanio can be seen in figures 18-20. x440. Slide No. 15514, Museum of Paleontology, University of Michigan.

PLATE 24



TRACY'S FERNS OF MISSOURI

BENJAMIN FRANKLIN BUSH

It is now fifty years since Tracy began collecting notes and material for his Catalogue of Plants of Missouri which was published in 1886.

In this Catalogue Tracy gives an account of all the Ferns and Fern Allies known to occur in the State, comprising 23 genera and 50 species, reported by 13 collectors, of which I am the only survivor. These collectors report 50 localities, incidentally exactly the same number as that of the species.

A comparison of Tracy's list with the latest account of Ferns and Fern Allies of Missouri may be interesting at this time. I shall make notes on the species in the order presented by Tracy, and shall use his names.

There are apparently 7 species included by Tracy in his Catalogue, that have not yet been collected in Missouri. This reduces the number of known species to 43, still a respectable list for that time.

The following is a list of Tracy's Ferns and Fern Allies:

1. *Equisetum arvense* L.—Tracy says this is common, but he must have had in mind only the Missouri and Mississippi River regions, since this species is almost unknown in southern Missouri and the prairie counties of the northern part of the state.

2. *Equisetum sylvaticum* L.—Reported from Greene County by Shepard, but evidently an error of determination, as this species has not yet been collected in Missouri.

3. *Equisetum robustum* Braun.—Probably identical with the present species of this name.

4. *Equisetum robustum affine* Engelm.—Probably correct, as it is common to all the Missouri River region.

5. *Equisetum hyemale* L.—Evidently our *E. laevigatum*, which was regarded as *E. hyemale* by most writers at the time Tracy published his Catalogue. Tracy did not recognize *E. laevigatum*, although it is abundant along all the big river bottoms in the state.

6. *Ophioglossum vulgatum* L.—The same as our present species, except that the report of Jackson County by Bush was based on *O. Engelmanni*. Tracy evidently not knowing *O. Engelmanni*, did not include it in his catalogue.

7. *Botrychium ternatum* Swz.—I have no idea what Broadhead found in Vernon County, but I am assuming it was what we now know as *B. obliquum*.

8. *Botrychium ternatum lunarioides* Milde.—Not the eastern species, which was never found so far west. I have no idea what Tracy had in mind when he listed this species which he says is common.

9. *Botrychium virginianum* Swz.—This species of *Botrychium* is common throughout the state. Tracy supposed that it was uncommon and records it for three counties.

10. *Botrychium matricarifolium* Braun.—Not the species of the east, which has never been found so far west as Missouri.

11. *Polypodium incanum* Swz.—Evidently our *P. polypodioides*, and thought by Tracy to be more restricted in the state.

12. *Polypodium vulgare* L.—Apparently but little known to Tracy at that time, and still imperfectly known from the hilly and Ozark counties in southern Missouri.

13. *Notholaena dealbata* Kunze.—Comparatively common in southern and western Missouri, although Tracy reports it from only two counties.

14. *Adiantum capillus-veneris* L.—Fairly common in the Ozark Counties.

15. *Adiantum pedatum* L.—Common to all the hilly and wooded counties, but more or less rare in northern Missouri, especially in the prairie counties.

16. *Pteris aquilina* L.—Common in all the Ozark counties, but more or less rare north of the Missouri River. Evidently some species of *Pteris*.

17. *Cheilanthes lanuginosa* Nutt.—Probably the same as *C. Feei*, and more or less common to all the Ozark counties.

18. *Cheilanthes tomentosa* Link.—Cited for Cole County in Wheeler's report, but so far no specimens have been seen from the state.

19. *Cheilanthes vestita* Swz.—Had about the same range in the state as *C. lanuginosa*, and probably more common.

20. *Pellaea atropurpurea* Link.—Common throughout the Ozark counties and along rocky bluffs of the larger rivers elsewhere.

21. *Pellaea gracilis* Hook.—I do not know what species Tracy had in mind when he listed this species, but I suspect that it might have been *P. glabella*, which Tracy did not recognize.

22. *Woodwardia virginica* Smith.—I cannot imagine what species Tracy had in mind, but I suspect that it might have been *Onoclea sensibilis*, which is sometimes labeled *W. virginica*, and is sometimes common.

23. *Asplenium angustifolium* Michx.—Probably identical with our species of the same name.

24. *Asplenium ebeneum* Ait.—Probably correctly identified. It is common in the Ozark counties, but rare or absent from the prairie counties in northern Missouri.

25. *Asplenium ebenoides* Scott.—Identical with the present species.

26. *Asplenium Filix-foemina* Bernh.—As listed by Tracy, included several species now separated.

27. *Asplenium parvulum* M. & G.—Correctly named so far as the Greene and Christian Counties are concerned, but the Jackson County report by Bush, was based on a collection of *A. platyneuron*.

28. *Asplenium pinnatifidum* Nutt.—Probably the species we now recognize.

29. *Asplenium thelypteroides* Michx.—Listed as common by Tracy, but appears to occur only in a few counties of the St. Louis region.

30. *Asplenium trichomanes* L.—Probably not occurring in Miller and St. Louis Counties, as given by Tracy, but is rarely found on boulders in the Ozark counties.

31. *Camptosorus rhizophyllus* Link.—No doubt correct, as it is very common on both limestone and sandstone boulders in the hilly or wooded counties.

32. *Phegopteris hexagonoptera* Fee.—No doubt correct, but the distribution of this species is from Marion County to southwestern Missouri, mostly in the Ozark counties.

33. *Aspidium aerostichoides* Swz.—No doubt correct, as it is very common in the hilly or wooded counties in southern Missouri.
34. *Aspidium Lonchitis* Swz.—Certainly not this species. Probably a misidentification of *A. acrostichoides*.
35. *Aspidium marginale* Swz.—More or less distributed throughout the Ozark counties on sandstone boulders and barrens.
36. *Aspidium spinulosum* Swz.—I cannot be sure what species of *Aspidium* Tracy and Letterman had at that time, but it must have been either *Thelypteris spinulosa* or *T. dilatata*.
37. *Aspidium Thelypteris* Swz.—Evidently correctly named, but more common than Tracy supposed.
38. *Cystopteris bulbifera* Bernh.—Tracy says this is common, but it is not found in the prairie regions of Northern Missouri, and appears to be confined to the Ozark counties.
39. *Cystopteris fragilis* Bernh.—Less common or almost absent from the prairie regions of northern Missouri.
40. *Onoclea sensibilis* L.—More common in the wooded counties, rare in the prairie regions of northern Missouri.
41. *Woodsia obtusa* Torr.—Common where there are outcrops of limestone, and sometimes on sandstone in the Ozark counties.
42. *Dicksonia pilosiuscula* Willd.—Evidently rare in Missouri, as it apparently has been found only in three counties in the extreme eastern part of the state.
43. *Osmunda cinnamomea* L.—Perhaps very rare or local, in the territory along the upper Mississippi River, and up the Missouri to the central part of the state.
44. *Osmunda Claytoniana* L.—Certainly not well-known to Tracy, as it ranges from St. Louis to Jackson and Vernon Counties and n[illegible]d to Clark County.
45. *Osmunda regalis* L.—Mostly in the Ozark counties, west to Ver[illegible] County, not found north of the Missouri River, or in the prairie counties.
46. *Azolla caroliniana* Willd.—Abundant in sloughs, lakes and ponds in the bottoms along the Mississippi and Missouri Rivers.
47. *Lycopodium dendroideum* Michx.—I can not be sure what Broadhead collected in Madison County, but I am assuming that it was *L. complanatum flabelliforme*, as that species is known to occur in that county.
48. *Selaginella rupestris* Spring.—Widely dispersed over the southern part of the state on limestone barrens, boulders and bluffs, mostly in the Ozark counties.
49. *Isoetes echinospora Braunii* Engelm.—Probably *I. melanopoda*, which Tracy does not list, as *I. Braunii* is a northern species and does not occur as far south as Missouri.
50. *Isoetes Engelmanni* Braun.—Tracy obtained his report of this species from Gray's Manual, which evidently was based on the original collection of Engelmann.

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